University of Alberta

The influence of trophic state, thermal structure and winterkill on littoral macroinvertebrate communities in Boreal Plain lakes

by

Peter William Langlois

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

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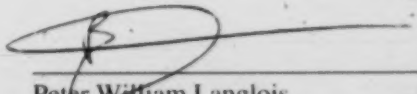

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ABSTRACT

Littoral macroinvertebrates were sampled from seven lakes varying in trophic state and thermal structure in north-central Alberta's Boreal Mixedwood ecoregion. Across the seven lakes, macroinvertebrate taxonomic richness was inversely related to total phosphorus concentration, and community diversity was positively related to thermal stability. Macroinvertebrate communities in less nutrient-rich, thermally stratified lakes, generally had higher relative biomass and density of amphipods and lower relative biomass and density of dipterans than communities in nutrient-rich, polymictic lakes. Total macroinvertebrate biomass was positively associated with total phosphorus concentration in stratified lakes only, suggesting that factors such as low dissolved oxygen availability negatively influence community structure in polymictic lakes. In the four study lakes with pike (*Esox lucius*) and perch (*Perca flavescens*) assemblages, including one that experienced a winterkill during the study, the density of *Gammarus* sp. and *Hyallela* sp. varied inversely with fish density (either measured or projected) over time, suggesting that benthivorous fish may directly influence the density of larger, common macroinvertebrate prey. Observed relationships between littoral macroinvertebrate community structure, total phosphorus concentration, and water column thermal stability suggest that enhanced eutrophication or climatic warming could negatively affect benthic food webs in boreal lakes.

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Chapter 1

1.1 General Introduction

Benthic macroinvertebrates provide a critical energy pathway in the food webs of north temperate lakes. They consume detritus (Wetzel, 1983; Batzer, 1998) and are, in turn, consumed by fish (Chapman, Mackay & Wilkinson, 1989; Price, Tonn & Paszkowski, 1991) and waterfowl (Hanson & Butler, 1994; Lillie & Evrard, 1994). Benthic macroinvertebrates are ubiquitous, relatively sedentary, long-lived, and inexpensive to sample (Rosenberg & Resh, 1993). In addition, macroinvertebrate community structure has been observed to reflect chemical, physical and biological habitat characteristics. Consequently, these communities have been widely accepted as indicators of habitat disturbance and water quality (Plafkin *et al.*, 1989; Rosenberg & Resh, 1993). Thus, macroinvertebrate communities are important to both the function and the understanding of aquatic ecosystems.

Lakes on the Boreal Plain of western Canada are shallow, nutrient rich systems, in comparison to lakes in other north temperate regions (Mitchell & Prepas, 1990). In addition, lakes on the Boreal Plain are ice-covered for five to six months a year and are located in a semi-arid region (Mitchell & Prepas, 1990). Because of these differences, macroinvertebrate habitat characteristics deemed critical to communities in other north temperate regions may or may not contribute to community structure in lakes on the Boreal Plain. Large areas of north-central Alberta's Boreal Plain have recently been leased for development by the forest products industry and over a longer period by the oil and gas industry. In other north temperate regions, research has shown that land clearing, in particular for timber harvest, can result in increased nutrient concentrations, primary

productivity, and dissolved oxygen consumption in lakes (Likens & Bormann, 1974; Rask, Arvola & Salonen, 1993). Whole-lake and in-lake mesocosm fertilization experiments have shown that increased nutrient concentrations and primary productivity can lead to increased macroinvertebrate biomass and density (*e.g.*, Welch, Jorgenson & Curtis, 1988; Blumenshine *et al.*, 1997; Clarke, Knoechel & Ryan, 1997). In addition, dissolved oxygen stress under ice-cover can alter predator-prey regimes through winterkill of fish populations in north temperate lakes (Tonn & Magnuson, 1982). Land clearing could increase the frequency of winterkill in lakes on the Boreal Plain by contributing to increased nutrient concentration followed by increased primary production and organic material available for decomposition thus leading to higher rates of under-ice dissolved oxygen consumption. Thus, land clearing has the potential to influence benthic food webs in lakes on the Boreal Plain in both 'bottom-up' and 'top-down' directions.

The primary objective of this project was to investigate the relationships between littoral macroinvertebrate community structure and natural among-lake gradients in environmental variables such as total phosphorus (TP) concentration, thermal stability, macrophyte biomass, sediment organic content, and basin slope. During the study, one lake experienced a winterkill. This allowed for the description of macroinvertebrate density before and after a substantial reduction in predatory fish density, and provided insight regarding the relative importance of fish and top-down trophic interactions in structuring littoral macroinvertebrate communities. This chapter reviews the published relationships between macroinvertebrates and the aforementioned environmental

variables. It also summarizes information on the potential impacts of forest harvest on lentic macroinvertebrate community structure.

1.2 Biogeochemical determinants of macroinvertebrate community structure

Most research on macroinvertebrate assemblages of north temperate lakes has focused on either the description of variation in community structure within lakes or the construction of empirical models designed to predict macroinvertebrate biomass based on key limnological parameters. Within lakes, variables that account for differences in macroinvertebrate community structure and biomass include water-column TP concentration (Dermott *et al.*, 1977), available macrophyte habitat (Hanson, 1990), sediment organic content (Nalepa & Thomas, 1976), and littoral zone slope (Rasmussen, 1988). Among lakes, observed differences in macroinvertebrate community structure and biomass have been attributed to TP concentration (Rasmussen & Kalff, 1987), sediment organic content (Dermott, 1988), and fish predation (Dermott, 1988). Despite this knowledge, the physical heterogeneity of the littoral zone has limited the understanding of whole-lake trends in littoral macroinvertebrate community structure and contributed to the relative lack of knowledge in comparison to stream macroinvertebrate communities (Rasmussen, 1988; Mackay, 1995).

Phosphorus ---The bottom-up influences of TP on pelagic food webs in north temperate lakes are well recognized. Studies of the pelagic zone have related the biomass of primary producers (Dillon & Rigler, 1974), zooplankton (Hanson & Peters, 1984), and fish to mean summer TP concentrations (Hanson & Leggett, 1982). In addition, TP

concentration has been used to successfully predict profundal (Hanson & Peters, 1984; Rasmussen & Kalff, 1987; Dinsmore, Scrimgeour & Prepas, 1999), and sublittoral (Rasmussen & Kalff, 1987) macroinvertebrate biomass. Dermott *et al.* (1977) observed higher chironomid density and biomass in the littoral zone of regions within Lake Memphremagog, Quebec, where TP concentrations were higher and algal blooms were more frequent as a result of point source sewage input. Many littoral macroinvertebrates are dependent on organic matter that settles to or grows on the lake bottom for food (Jónasson, 1978; Batzer, 1998). The coupling of high TP concentrations, high primary productivity, and macroinvertebrate dependency on settling matter for food suggests that littoral community biomass may be positively related to TP concentration in lakes on the Boreal Plain. Literature dealing with macroinvertebrate-phosphorus relations has dealt primarily with nutrient-poor lakes (*e.g.*, Hanson & Peters 1984; Rasmussen & Kalff, 1987). An improved understanding of the link between trophic state and benthic food webs in nutrient-rich systems would be obtained by analyzing littoral macroinvertebrate community structure in lakes on the Boreal Plain.

Macrophyte assemblages --- Submerged macrophytes contribute to macroinvertebrate community structure by providing food, refuge from predators, and three-dimensional heterogeneity of habitat. In two Florida (U.S.A.) lakes, macrophytes increased substrate heterogeneity and macroinvertebrate resources by providing root masses and litter from dead plant matter (Schramm & Jirka, 1989). Macrophytes reduce predator efficiency (Gilinsky, 1984; Diehl, 1992) and moderate physical disruption of the water-column and sediments, leading to higher macroinvertebrate densities in vegetated regions of lake littoral zones (Beckett, Aartila & Miller, 1991). In Toolik Lake, Alaska,

sculpin were more successful foraging for chironomids in exposed sediments, relative to protected sediments of macrophyte beds (Hershey, 1985). For Narrow Lake, Alberta, it was hypothesized that the dense and highly branched physical structure of *Chara* spp. increased available habitat and therefore macroinvertebrate biomass, relative to rooted macrophyte beds (Hanson, 1990). In Lake Memphremagog, macrophyte beds were more developed and macroinvertebrate densities were higher in littoral regions of low wave exposure and slope, relative to littoral regions of higher wave exposure and slope (Rasmussen, 1988). These studies all focused on variation in macroinvertebrates and macrophytes within lakes. Few, if any studies, have attempted to describe relationships between macroinvertebrates and macrophytes among a set of lakes. A comparison of macroinvertebrate community structure and average macrophyte biomass across a gradient of lakes may enhance the understanding of the influence of macrophytes on benthic macroinvertebrate community structure.

Sediment composition --- Many benthic macroinvertebrates feed on dead and decaying plant and animal matter (Wetzel, 1983; Mann, 1989). In addition, some macroinvertebrates use material found in bottom sediments for tube and case construction (McLachlan, 1969; Clifford, 1991). Within Lake Geneva, Switzerland, oligochaete and nematode densities were higher in sediments rich in organic content, relative to sediments poor in organic content (Lang, 1988). Among several northwestern Ontario lakes, total macroinvertebrate density was higher in lakes with higher sediment organic content, in comparison to lakes with sediments of lower organic content (Dermott, 1988). Amphipods and chironomids depend on the organic content of surficial sediments as a primary food source and are numerically dominant taxa in lakes on Alberta's Boreal

Plain (Clifford, 1991; Yee, 1997). Thus, a comparison of macroinvertebrate community structure across a set of lakes varying in average sediment organic content could yield valuable information pertaining to the dependency of macroinvertebrates on sediment organic matter.

Basin morphometry --- The shape of a lake's surface and the slope of the littoral zone are both important contributors to macroinvertebrate habitat. In the Turkey Lakes, Ontario, depth and wave exposure were key factors contributing to macroinvertebrate biomass (Dermott, 1988). Further, wave exposure accounted for differences in taxonomic richness of Coleoptera among 98 Swedish lakes (Nilsson & Soderberg, 1996). In Lake Memphremagog, detailed measurement of site-specific littoral zone slope and community structure suggested that zones of greater wave exposure and greater slope had lower macroinvertebrate biomass in comparison to regions of lesser wave exposure and slope (Rasmussen, 1988). Sediment organic loads and macrophyte beds were also directly influenced by littoral zone slope and wave exposure in Lake Memphremagog, with areas of greater slopes accumulating less organic matter and fewer rooted macrophytes. This would result in steep-sloped littoral zones having less food and refuge for macroinvertebrates. The tight linkages that exist between external processes (*e.g.*, wind), basin morphometry, and macroinvertebrate biomass have been illustrated through this work. However, little or no research has been conducted on among-lake relationships between average littoral slope and macroinvertebrate community structure.

Fish predation --- Macroinvertebrates are a critical food source for fish (Jónasson, 1978; Mittlebach, 1988). The importance of macroinvertebrates in the diet of common Boreal Plain fishes such as the fathead minnow (*Pimephales promelas*), yellow perch

(*Perca flavescens*), northern pike (*Esox lucius*), and white sucker (*Catostomus commersoni*) is well documented (Price *et al.*, 1991; Post & Cucin, 1984; Beaudoin *et al.*, 1999; Ahlgren, 1990, respectively). However, study of the response of macroinvertebrate communities to varying levels of fish predation has yielded conflicting results. Whole-lake fish introduction and removal experiments have suggested that tight linkages exist between macroinvertebrate density and fish predation. Some mesocosm experiments have suggested that only the density of larger, preferred–prey taxa are affected through predation by fish. Total biomass, richness, and mean size in the littoral macroinvertebrate community were reduced by introduction of yellow perch into a previously fishless lake (Post & Cucin, 1984). Macroinvertebrate density increased following fish population removal by rotenone treatment (Ball & Hayne, 1952; Hanson & Butler, 1994). Macroinvertebrate and fish biomass were inversely proportional when compared among the Turkey lakes, Ontario (Dermott, 1988). The density of large macroinvertebrates was reduced by fish, especially at high fish densities in experimental ponds (Crowder & Cooper, 1982; Merrick, Hershey & McDonald, 1985; Mittlebach, 1988).

In contrast, some studies have concluded that the link between fish and littoral macroinvertebrate community structure is weak. No detectable differences in macroinvertebrate communities were observed between cages with and without fish in Par Pond, North Carolina (Thorp & Bergey, 1981). Macroinvertebrate community structure was not affected by removal of 85% of the fish in an experimental pond (Pierce & Hinrichs, 1997). No differences in macroinvertebrate communities due to yellow perch predation were detected by Cobb and Watzin (1998). It has also been shown that

the interaction between macroinvertebrate communities and fish predators is limited by available macrophyte cover (Crowder & Cooper, 1982; Gilinsky, 1984; Diehl, 1992). A large gap remains in our understanding of the control fish predation can have on the community structure of littoral macroinvertebrates.

During this study, one lake experienced a winterkill, losing the majority of its pike and perch. Winterkill is a natural phenomenon in north temperate lakes (Tonn & Magnuson, 1982). As such, the effects of winterkill on fish communities are relatively well documented (*e.g.*, Casselman & Harvey, 1975; Tonn & Paszkowski, 1986). However, the subsequent response of macroinvertebrate communities to this change in predation pressure has not been reported for lakes on the Boreal Plain. Observation of macroinvertebrate density before and after winterkill may contribute to our understanding of the effects of fish predation on benthic food webs in lakes.

1.3 Potential habitat change and macroinvertebrate community response

Large tracts of land have been leased for timber harvest in north-central Alberta. Interactions of man with nature regularly result in reduced biological diversity and increased transport of nutrients within disturbed ecosystems (Rapport, Regier & Hutchinson, 1985). The use of species rich assemblages, such as macroinvertebrate communities, as indicators of ecosystem disturbance can be effective because various member species exhibit consistent differences in tolerance and survivorship (Schindler, 1987; Gray, 1989). An extensive literature addresses the effects of forest harvest on stream habitats and macroinvertebrates (*e.g.*, Newbold, Erman & Roby, 1980; Hartman &

Scrivener, 1990; Growns & Davis, 1991) and some studies address effects on lake habitats (*e.g.*, Likens & Bormann, 1974; Rask *et al.*, 1993). However, little information exists on the responses of lake ecosystems and littoral macroinvertebrates to timber harvest on the Boreal Plain.

Documented watershed responses to forest harvest include: elevated water tables (Bosch & Hewlitt, 1982), and increased transport of phosphorus (Hobbie & Likens, 1973) and dissolved organic matter to lakes (Likens *et al.*, 1970; Likens & Bormann, 1974). Nutrient and chlorophyll *a* concentrations, mixing depths, and epilimnetic temperatures all increased, and dissolved oxygen concentration decreased, in a small lake in Finland following logging and fire in its watershed (Rask *et al.*, 1993). Timber harvest could result in elevated phosphorus concentration in lakes on the Boreal Plain.

Little information exists on the response of littoral macroinvertebrate communities to increased phosphorus concentrations in natural ecosystems. However, some forestry related and whole-lake and mesocosm fertilization experiments have been conducted. Littoral zone macroinvertebrate biomass increased approximately two-fold after phosphorus concentration was increased from 10 to 150 ppb, in a small, oligotrophic lake (Smith, 1969). Emergent chironomid density and biomass doubled in the first and subsequent years of a six-year fertilization study where nutrient additions resulted in a doubling in phtyoplankton biomass in two arctic lakes (Welch *et al.*, 1988). Further, total biomass of the amphipod *Gammarus lacustris lacustris* (G.O. Sars) increased four-fold during the same experiment (Jorgenson, Welch & Curtis, 1992). The density of sediment dwelling chironomids doubled after nine weeks of fertilization resulted in an increase in TP concentration from 10 to 25 $\mu g\ L^{-1}$ in experimental mesocosms in Long Lake,

Michigan (Blumenshine *et al.*, 1997). The density of most macroinvertebrates increased measurably during three years of elevated nutrient loading in Coles Pond, Newfoundland (Clarke, Knoechel & Ryan, 1997). Thus, macroinvertebrate communities of lakes on the Boreal Plain may be influenced by forest removal, should it lead to sustained elevated phosphorus concentrations and associated increases in primary production.

1.4 Summary and research objectives

In 1993, a seven-year study designed to study the impacts of forest harvest on terrestrial and aquatic ecosystems in the aspen-dominated mixed-wood forest of Alberta was initiated. Key objectives included detailed description and development of current understanding of these understudied systems, and testing the ability of riparian 'buffer-strips' of intact forest to mitigate and/or moderate the impacts of forest harvest on Boreal Plain ecosystems. Terrestrial and Riparian Organisms, Lakes and Streams (TROLS) was a large, multi-sector study designed to further our understanding of the land-water interface and lead to practical application of this knowledge. The lake portion of TROLS focused on 12 lakes divided equally among three regions (Lac La Biche, South Calling Lake, and South Pelican Hills) of north-central Alberta. Following site selection and two years of pre-harvest study, one lake from each region was scheduled to be harvested to within either 20-, 100-, 200-, or 800-m during the winter, and monitored for another three years.

The work described in this thesis was conducted primarily in the final pre-harvest year (1996) and the first post-harvest year (1997) of the TROLS study. The primary objective of this study was to determine how macroinvertebrate community structure

relates to environmental variables among lakes on the Boreal Plain. The second objective was to investigate the response of a littoral macroinvertebrate community to winterkill of pike and perch.

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Chapter 2
LITTORAL MACROINVERTEBRATE COMMUNITIES: RELATIONSHIPS WITH TROPHIC STATE AND WATER-COLUMN THERMAL STRUCTURE IN BOREAL PLAIN LAKES

2.1 Introduction

Littoral macroinvertebrates are major consumers of algae and detritus and are themselves an important food resource for fish (Jónasson, 1978; Mittlebach, 1988) and waterfowl (Swanson & Nelson, 1970; Lillie & Evrard, 1994). Macroinvertebrates are also effective indicators of water quality, due to varying tolerances to environmental stress within communities (Saether, 1979; Rosenberg & Resh, 1993). Environmental variables such as total phosphorus (TP) concentration (Dermott *et al.*, 1977; Rasmussen & Kalff, 1987), macrophyte habitat (Hanson, 1990), sediment organic content (Dermott, 1988), and littoral zone slope (Rasmussen, 1988a; Rasmussen & Rowan, 1997), have all been deemed important to macroinvertebrate community structure in the littoral zone. Despite their relative importance, our understanding of littoral macroinvertebrate communities and their relationships with the chemical, physical, and biological environment is limited, perhaps due to the heterogeneous nature of the littoral zone (Rasmussen, 1988a; Harrison & Hildrew, 1998).

The degree to which the structure of littoral macroinvertebrate communities is determined by TP concentration and associated bottom-up food web effects can be influenced by other factors. In oligotrophic lakes, littoral macroinvertebrate density and biomass are positively related to TP concentration (Smith, 1969; Dermott *et al.*, 1977; Welch, Jorgenson & Curtis, 1988; Clarke, Knoechel & Ryan, 1997). Macroinvertebrate food resources in oligotrophic lakes are limited by primary production, which, in turn, is

generally limited by TP concentration. In contrast, littoral macroinvertebrates may be negatively related to TP concentration in hypereutrophic lakes, where low concentrations of dissolved oxygen can reduce oxygen-rich habitat (Wetzel, 1983; Takamura & Iwakuma, 1990). Littoral macroinvertebrate biomass was not detectably related to TP concentration when compared across a gradient of lakes ranging from oligotrophic to hypereutrophic (Rasmussen & Kalff, 1987). However, sublittoral macroinvertebrate biomass was positively related to TP concentration across a similar range of lakes (Rasmussen & Kalff, 1987). Differences in macroinvertebrate habitat between littoral and sublittoral habitats (*e.g.*, macrophyte cover, water temperature) may account for this dichotomy (Rasmussen & Kalff, 1987). Littoral macroinvertebrate communities in mesotrophic to hypereutrophic lakes potentially inhabit an environment where the benefits of high TP concentration begin to be offset by the adverse effects of low concentrations of dissolved oxygen. Thus, the relationship between littoral macroinvertebrate community structure and TP concentration in these lakes is also likely to be dependent on other factors that contribute to dissolved oxygen concentration, such as primary producers, morphometry, and thermal structure of the water column.

Littoral macroinvertebrate habitat in temperate regions can differ markedly between lakes that develop thermal stratification either intermittently or not at all (polymictic) and those that maintain thermal stratification during summer (stratified). Relative to stratified lakes, polymictic lakes tend to be shallow, have gradually-sloped basins, and have greater macrophyte biomass (Duarte & Kalff, 1986). As shallow systems, polymictic lakes also have higher primary production and are more susceptible to under-ice depletion of dissolved oxygen, than stratified lakes (Barica & Mathias, 1979;

Fee, 1979; Riley & Prepas, 1982; Babin & Prepas, 1985). Furthermore, lakes with high macrophyte biomass can have extreme diel fluctuations in dissolved oxygen concentration in the littoral zone during summer (Wetzel, 1983; Davies & Gates, 1991). Polymictic lakes may thus offer littoral macroinvertebrates habitat that is more environmentally harsh in comparison to stratified lakes. The littoral macroinvertebrate communities of stratified, nutrient-poor lakes, might then be expected to have higher numbers of organisms that are intolerant of low dissolved oxygen concentrations, relative to those of nutrient-rich, polymictic lakes.

Lakes in the Boreal Mixedwood ecoregion (Boreal Plain) of north-central Alberta range in trophic state from mesotrophic to hypereutrophic and vary in the degree to which they are thermally stratified during summer (Mitchell & Prepas, 1990). In addition, nutrient inputs and water-column thermal structure in lakes on the Boreal Plain may change due to human activity in the region. Watersheds in this region of Alberta are being rapidly developed for timber and petroleum / natural gas extraction, potentially altering nutrient concentrations in lakes. Removal of riparian forest could also result in enhanced wind-action upon lake-surfaces, deepening of thermoclines, and perhaps weakening of thermal stratification in shallow lakes where further deepening of thermoclines could eliminate stratification entirely. The thermal stratification of lakes on the Boreal Plain could weaken under a climatic warming scenario. In lakes on the Canadian Shield, a 20-year period of climatic warming was associated with deeper thermoclines as a result of increased water clarity, deeper light penetration, and warmer water temperatures (Schindler *et al.*, 1996; Fee *et al.*, 1996). The relatively undisturbed status of watersheds of lakes on the Boreal Plain, combined with recently accelerated

land clearing, renders the study of littoral macroinvertebrate communities as they relate to trophic state and thermal structure particularly relevant.

My research was conducted in lakes on the Boreal Plain varying naturally in trophic state (total phosphorus (TP) concentration), summer thermal structure, macrophyte biomass, basin slope, and sediment organic content. I tested whether littoral macroinvertebrate: (I) taxonomic richness and community diversity were inversely related to trophic state and positively related to thermal stability; (II) total biomass and trophic state were positively related; and (III) communities of thermally unstable (polymictic) lakes were numerically dominated by taxa tolerant of environmentally harsh conditions (*e.g.* Dipteran larvae) relative to communities of thermally stable (stratified) lakes.

2.2 Materials and Methods

Description of study lakes

The study sites comprise a subset of 7 of 12 lakes from 'Terrestrial and Riparian Organisms Lakes and Streams' (TROLS). TROLS was an inter-disciplinary study designed to assess the importance of riparian buffer strips in moderating timber harvest impacts on terrestrial and aquatic ecosystems. The lakes are located on the Boreal Plain, in three aspen-dominated watersheds of north-central Alberta's Boreal Mixedwood ecoregion: two lakes are near Lac la Biche (LLB); two are near South Calling Lake (SCL); and three are near South Pelican Hills (SPH) (Fig. 2.1; Table 2.1). Study lakes are named according to region and planned buffer width between the lake and harvested blocks (*e.g.*, SCL20 = lake in SCL region scheduled to maintain a 20-m buffer). A small

portion of the watershed of LLB800 was harvested for timber prior to my study. With the exception of SCL800, parts of the watersheds of the remaining lakes were harvested between November 1996 and March 1997. These lakes are typically ice-covered for six months of the year (November to April), are small (55 to 157 ha surface area) and shallow (1.3 to 5.2 m mean depth, 2.2 to 11 m maximum depth), and include systems that thermally stratify between spring and fall overturn periods (stratified), as well as those that stratify intermittently or not at all during the summer (polymictic) (E.E. Prepas, unpublished data) (Table 2.1). Total regional precipitation was high in 1996 (591 mm), and typical in 1997 (453 mm), in comparison to the long-term (1971-1998) average of 481 mm (Environment Canada, unpublished data). Fish communities consisted of either minnows and brook stickleback, or pike, perch, and in some cases white sucker (W. Tonn and A. Danylchuk, unpublished data) (Table 2.1). Stable isotope and stomach content analyses has shown that these fish assemblages can depend on macroinvertebrates for food (Beaudoin, 1998; Beaudoin *et al.*, 1999). A late-spring 1996 winterkill culled 80 to 90 % of the pike and perch population in LLB800 (W. Tonn and A. Danylchuk, unpublished data). Subsequent gillnet (1997 and 1998) and beach seine (1998) surveys in LLB800 suggested that fish densities were low but recovering during 1997 (W. Tonn, unpublished data).

Methods

Benthic samples were collected once immediately following ice-out (7 to 28 May 1996), and twice in mid-summer (27 July to 7 August 1996, 11 to 16 August 1997). Samples were collected with a 232-cm^2 Ekman-Birge grab, fitted with 500-µm mesh top-screen, at depths ranging from 1.5 to 3 m below the water surface (mid-littoral zone), where

macrophytes did not interfere with dredge closure. Samples were discarded and re-taken when macrophytes interfered with dredge closure. On each sampling trip, six samples were collected per lake. All six samples were subsequently picked and enumerated for density estimates, while five of the six were further processed for dry mass estimates. The remaining undried sample from each lake and each sampling period was archived for identification reference purposes.

Grab contents were sieved in the field through a 200-µm Nitex bag and preserved in 4 % formalin solution. Samples were sieved through 4- and 1-mm, and 250-µm meshes in the laboratory. Prior to picking, small size fractions (1 mm and 250 µm) from samples high in fine detritus were centrifuged and floated in sugar solution, following Cromar & Williams (1991), to facilitate separation of invertebrates from detritus. Macroinvertebrates were picked under low power dissecting microscope and identified to family following keys by Clifford (1991). Analysis of quantitative descriptors of macroinvertebrate community structure at the family-level can produce comparable results to analysis at the genus-level (Warwick, 1988; Bowman & Bailey, 1997). The only members of Gammaridae and Hyallelidae in Alberta are *Gammarus lacustris* and *Hyallela azteca* (Clifford, 1991), thus these families are referred to in the text independently as *Gammarus* sp. and *Hyallela* sp. and collectively as amphipods. Several taxa were identified only to either phylum (Bryozoa, Platyhelminthes), subclass (Acari, Oligochaeta), or order (Nematoda). To determine dry mass, macroinvertebrates were oven-dried at 60°C for 24 h and weighed to the nearest 0.1 mg on a Mettler AT261 Deltarange balance. The Shannon-Wiener Index of diversity (H') was calculated as:

$$H' = - \Sigma_{(i=1:s)} P_i \ln P_i$$

where P_i is the proportion of individuals contributed by taxon i to the total number of individuals in the sample, and S is the total number of taxa in the sample (Shannon & Weaver, 1949). The percentage similarity index was calculated as:

$$P = \Sigma \text{ minimum } (p_{1i}, p_{2i})$$

where P = percent similarity between samples 1 and 2, p_{1i} = percentage of taxon i in community sample 1, and p_{2i} = percentage of taxon i in community sample 2 (Krebs, 1989).

Deep-site temperature and dissolved oxygen concentration data, as well as euphotic zone water samples (three sites) for TP analysis, were collected at three-week intervals from June to August of 1996 and 1997 (E.E. Prepas, unpublished data). The closest sampling date in time, either before or after mid-summer macroinvertebrate samples were collected, was selected as the cut-off for calculation of mean summer TP concentration. TP concentration was determined following the modified Menzel and Corwin (1965) potassium persulfate method (Prepas & Rigler, 1982). Temperature and dissolved oxygen concentration data were collected with a Yellow Springs Instruments Model 59 meter fitted with a battery-powered stirrer. The strength of thermal stratification (thermal stability (S)) was quantified as the amount of work required to mix a lake to uniform density without addition or subtraction of heat (Hutchinson, 1957). Thermal stability (S) was calculated from the average June to August temperature profile for each lake:

$$S = (A_0^{-1}) \int_{z_0:z_m} (\rho_z - \rho_1)(A_z)(z - z\rho_1)\, dz$$

Where: A_0= the surface area in square centimetres; A_z= the area (cm^2) at depth z (considered positive and in centimetres); ρ_1= the final or mean density that would result

from mixing the lake to uniformity (g cm^{-3}); ρ_z= the density at depth z; $z\rho_1$= the depth in cm where the final or mean density (ρ_1) exists prior to mixing; z_m= maximum depth in centimetres; z_0= surface, or zero depth. This method of calculating S was adapted from Idso (1973) and is described in further detail in Cole (1979). Where $S \geq 5.0$ g cm cm^{-2}, a lake is described as stratified, and where $S < 5.0$ g cm cm^{-2}, a lake is described as polymictic.

Except in SPH100, submerged macrophytes and surficial sediments were collected from all lakes in September 1997. To encompass the range of depths where macroinvertebrates were collected, submerged macrophytes were sampled with an Ekman dredge along four randomly selected transects, at the 1-, 2- and 3-m depth contours. Macrophytes were rinsed in a 200-µm Nitex bag to remove sediments and frozen for eight months. To determine dry mass, thawed macrophyte samples were dried for 24 h at 60°C and weighed to the nearest 0.01 g on a Mettler College 2440 Deltarange balance. Mean macrophyte dry mass (g m^{-2}) was calculated for each depth and the values for all depths were averaged to yield an estimate of submerged macrophyte biomass for the littoral zone of each lake.

Sediment samples were collected with a four-barrel Kajak-Brinkhurst remote corer. To span the depth range that macroinvertebrates were collected in, one pair of sediment cores (*i.e.* two of the four barrels) was collected from each of three randomly selected locations at depths between 1 and 3 m in each lake. Approximately 3 cm of surficial sediment from each barrel was poured into a watertight plastic bag and frozen for eight months. To determine wet mass, each pair of cores was thawed, sub-sampled, pooled, and weighed to the nearest 0.01 mg on a Mettler AT261 Deltarange balance. To

determine dry mass, pooled sub-samples were then frozen, freeze-dried, and re-weighed to the nearest 0.01 mg on a Mettler AE240 balance. Ashed mass was determined by further drying freeze-dried samples in previously heated and weighed evaporating dishes in a Ney Box muffle furnace at 550 °C for 1 h, after which samples were cooled in a dessication chamber for 30 min and re-weighed. % Water and organic content were then calculated:

% Water content = ((wet mass - dry mass) / dry mass) x 100

% Organic content = ((dry mass - ashed mass) / dry mass) x 100

The values for % water content and % organic content for each pooled pair of core samples from each lake were then averaged to yield estimates of sediment water and organic content for the littoral zone.

Mean littoral slope of each lake was estimated from bathymetric maps. At ten randomly selected shoreline points, the distance from shore to the point on the water surface directly above the 3-m depth contour was measured (2-m contour for SCL800 and SPH100, maximum depth < 3 m). Percent slope was calculated as the rise (3-m) over the run (distance from shore to point on water surface above 3-m depth contour) multiplied by 100. The values for littoral slope were then averaged and converted to percent slope to provide a mean for each lake.

To complement the data collected in this study, data from four other north-central Alberta lakes were obtained from Yee (1997): littoral macroinvertebrate biomass data for Jenkins, Crooked, and Baptiste lakes are pooled means of duplicate samples taken at 1- and 3-m depths in early August of 1991, 1992, and 1993; while Lofty Lake data are from August 1991. TP concentrations for Jenkins, Crooked, and Lofty lake water are from

Zhang & Prepas (1996), while for Baptiste Lake, data were provided by Reedyk, Prepas & Chambers (submitted, 1999).

Pearson correlations were generated between environmental and macroinvertebrate variables with community structure data collected during both mid-summer sampling periods. Because the macroinvertebrates that dominate littoral communities in Alberta lakes (*e.g.*, *Gammarus* sp., *Hyallela* sp., chironomids) are typically either uni- or multivoltine (Clifford, 1991), and some environmental variables can vary considerably from year to year, data collected from a given lake in both study years were treated as independent. Non-normally distributed data were transformed prior to parametric statistical analyses: macroinvertebrate variables (density, biomass, taxonomic richness, community diversity), TP concentration, thermal stability, depth, and macrophyte biomass data with $\log_{10}(x+1)$; macroinvertebrate relative density and biomass, sediment organic content, sediment water content, and littoral slope with arcsine square root. Whole-lake means of percent composition were compared between thermal mixing regimes by Mann Whitney *U*.

2.3 Results

On average, larval chironomids dominated total littoral macroinvertebrate density (>54%) (see Appendix A), but contributed less to total biomass (<14%). Oligochaetes, nematodes, amphipods and sphaerid clams represented a further 38% of total littoral macroinvertebrate densities (see Appendix A). Amphipods dominated total littoral macroinvertebrate biomass (>36%), and hirudineans (leeches) and sphaerid clams also

made substantial contributions (>30% combined). Total littoral macroinvertebrate densities were lowest during the May 1996 sampling period in all lakes ($t > 2.8$, df = 5, $P < 0.05$). Macroinvertebrate communities were in general dominated by amphipods and dipterans.

Wide ranges in TP concentration, thermal stability, and macrophyte biomass among the study lakes provided a basis to test for association of these variables with littoral macroinvertebrate community structure. Trophic state ranged from mesotrophic to hypereutrophic, with euphotic TP concentrations spanning 22 to 208 μg L^{-1} (Table 2.2, E.E. Prepas, unpublished data). Mean thermal stability spanned 0.4 to 93 g cm cm^{-2}: two lakes (SCL20, SPH20) were relatively strongly thermally stratified; two were weakly stratified (LLB800, LLB20); and the remaining lakes were consistently polymictic and only developed thermal stratification intermittently (Table 2.2, E.E. Prepas, unpublished data). Thermal stability was related to littoral slope ($r = 0.62$, $P < 0.05$), and maximum ($r = 0.94$, $P < 0.01$) and mean lake depth ($r = 0.86$, $P < 0.01$) (E.E. Prepas, unpublished data). Submerged macrophyte biomass was as high as 256 g m^{-2} and as low as 1.7 g m^{-2} among the study lakes (Table 2.2). Although submerged macrophyte biomass and thermal stability appeared to be negatively associated, the relationship was not significant ($P = 0.07$). Dissolved oxygen concentrations were less than 2.0 mg L^{-1} at depths of 2 to 3 m on at least one sampling date in polymictic lakes (SPH800, SPH100, SCL800), whereas dissolved oxygen concentrations less than 2.0 mg L^{-1} were never observed in this depth range in stratified lakes (E.E. Prepas, unpublished data). Sediment organic content was typically moderate (36 ± 7%) and sediment water content was generally high (78 ± 7%) (Table 2.2). Littoral slope ranged 9-fold among lakes, but was generally low (2.9 ±

0.7%) (Table 2.2). Narrow ranges in sediment characteristics and basin slope suggested that these variables were less likely to contribute to variation in littoral macroinvertebrate community structure among the study lakes.

Littoral macroinvertebrate communities were most strongly associated with TP concentration and thermal stability, and less strongly, but still correlated with macrophyte biomass and littoral slope among the study lakes (Table 2.3). Taxonomic richness was negatively related to TP concentration, as were the densities of *Gammarus* sp. and *Hyallela* sp. (Table 2.3). Total macroinvertebrate biomass appeared unrelated to TP concentration across all seven TROLS lakes, and several of the most nutrient-rich lakes had the lowest total macroinvertebrate biomass values (*e.g.*, SPH100, SCL800) (Fig. 2.2). Community diversity and *Gammarus* sp. and *Hyallela* sp. densities were positively related to thermal stability (Table 2.3), suggesting that they may also be linked to the thermal structure of the water column. *Hyallela* sp. biomass was inversely related to macrophyte biomass, while *Hyallela* sp. density was positively related to littoral slope (Table 2.3). In contrast, no littoral macroinvertebrate variables were detectably related to sediment organic content or sediment water content.

Littoral macroinvertebrate communities in lakes on the Boreal Plain differed when compared across mixing regimes. Littoral macroinvertebrate biomass and TP concentrations for stratified lakes from my study and from Yee (1997) were positively related ($r = 0.59$, $P < 0.05$) (Fig. 2.2). On the contrary, in polymictic lakes, littoral macroinvertebrate biomass and TP concentration were not detectably related ($P = 0.2$) (Fig. 2.2). Littoral macroinvertebrate biomass in stratified lakes on the Boreal Plain was higher for a given TP concentration, when compared with the relationship reported for

sublittoral macroinvertebrate biomass in north temperate lakes (Rasmussen & Kalff, 1987) (Fig. 2.2). These results indicate that the bottom-up influences of TP concentration may positively affect littoral macroinvertebrate communities in thermally stable, mesotrophic to eutrophic lakes.

Relative contributions to total biomass and density by *Gammarus* sp., *Hyallela* sp., and larval dipterans also appeared to be linked to TP concentration and thermal stability. The relative contributions to total biomass and density by *Gammarus* sp. and *Hyallela* sp. were negatively related to TP concentration and positively related to thermal stability, while relative dipteran densities were positively related to TP concentration and negatively related to thermal stability (Table 2.4). Thus, among the study lakes, TP-poor, thermally stratified lakes generally had higher relative amphipod density and biomass and lower relative dipteran density and biomass in comparison to TP-rich, polymictic lakes (Table 2.5). *Gammarus* sp. and *Hyallela* sp. relative biomasses were higher and relative dipteran biomass was lower in thermally stratified lakes (n = 8 in all cases), relative to polymictic lakes (n = 6 in all cases) ($z < -2.2$, $P < 0.05$, in all cases) (Table 2.5). In comparison, *Gammarus* sp. ($z = -1.4$, $P = 0.18$) and *Hyallela* sp. ($z = -1.9$, $P = 0.06$) relative densities were not detectably different between thermal regimes, while relative dipteran density was lower in stratified lakes ($z = -3.1$, $P < 0.01$) (Table 2.5). When littoral macroinvertebrate communities were compared across the lake gradient in thermal stability, communities from like mixing regimes (*i.e.*, either from stratified or polymictic lakes) were generally most similar (Table 2.6). Communities from opposite mixing regimes were generally least similar during both study years (Table 2.6 a; Table 2.6 b). In 1997, the littoral macroinvertebrate community in SPH100 was markedly dissimilar

from the other six study lakes, due to unusually high numbers of chaoborids in the samples. The relative paucity of amphipods and trend of numerical dominance by dipterans in polymictic lakes implicates these systems as environmentally harsh relative to stratified lakes.

2.4 Discussion

Littoral macroinvertebrate communities in lakes on the Boreal Plain consisted primarily of amphipods (*Gammarus* sp. and *Hyallela* sp.) and larval dipterans (Chironomidae, Chaoboridae). Total macroinvertebrate density was low in spring and high in mid-summer, suggesting that the communities of these lakes may cycle seasonally. Macroinvertebrate densities often peak in mid- to late-summer (Cooper, 1965; Wen, 1992; Yee, 1997). The littoral macroinvertebrate communities of lakes on the Boreal Plain are thus comparable in composition and seasonality to previously studied communities in north temperate lakes (Cooper, 1965; Wen, 1992; Yee, 1997). The relationships observed between macroinvertebrate communities, and trophic state and thermal stability, may have application in shallow lakes of similar trophic state elsewhere.

Negative relationships of littoral macroinvertebrate taxonomic richness and amphipod density with TP concentration have not been reported prior to this study. Reduced richness, reduced diversity, and shifts in community composition towards dominance by shorter-lived, opportunistic species, are typical responses to stress in ecological communities (Rapport, Regier & Hutchinson, 1985; Schindler, 1987; Gray, 1989). Dipteran larvae, such as Chironomidae, dominated communities in TP-rich,

polymictic lakes on the Boreal Plain, and are more tolerant of increasingly eutrophic conditions than most macroinvertebrates (Saether, 1979). Chironomidae also tend to have short life cycles, and thus are frequently the first organisms to respond to increased TP concentration during fertilization studies (Smith, 1969; Welch *et al.*, 1988; Blumenshine *et al.*, 1997; Clarke *et al.*, 1997). Patterns of reduced taxonomic richness across the positive gradient of TP concentration in lakes on the Boreal Plain imply that littoral macroinvertebrate assemblages experience higher environmental stress under increasingly TP-rich conditions.

The positive association between macroinvertebrate biomass and TP concentration in stratified lakes suggests that the bottom-up effects of TP concentration may positively influence benthic communities in thermally stable mesotrophic to eutrophic systems. These results contradict those of Rasmussen & Kalff (1987), who found that basin slope and water colour were better predictors of littoral macroinvertebrate biomass across lakes ranging widely in trophic status. However, these authors reported that sublittoral macroinvertebrate biomass was positively related to TP concentration across 87 north temperate lakes. Macroinvertebrates in nonvegetated sediments in the littoral and sublittoral zones are exposed to the water column and are likely to receive their food in the form of settling algae and detritus (Jónasson, 1978; Batzer, 1998). Littoral macroinvertebrate samples in my study and sublittoral samples in Rasmussen & Kalff (1987) were collected from macrophyte-free sediments above the thermocline; therefore the results should be comparable. However, sublittoral macroinvertebrate samples from Rasmussen & Kalff (1987) were collected only from sediments deeper than the depth of macrophyte colonization, while littoral

macroinvertebrate samples in my study were collected from sediments at shallower depths lacking vegetation. For a given TP concentration, littoral macroinvertebrate biomass in stratified lakes on the Boreal Plain was consistently higher than sublittoral macroinvertebrate biomass in north temperate lakes. Perhaps the metabolism-enhancing effects of warmer littoral habitats in stratified lakes on the Boreal Plain lead to higher macroinvertebrate biomass estimates relative to cooler sublittoral habitats in the north temperate lakes studied by Rasmussen & Kalff (1987). Biomass of profundal macroinvertebrates and water temperature are positively related in boreal lakes in this region (Dinsmore *et al.*, 1999).

In contrast to stratified lakes, littoral macroinvertebrate biomass was not detectably related to TP concentration among polymictic lakes. This suggests that any possible positive effects of high TP concentration on littoral macroinvertebrates were likely overcome by the negative effects of low dissolved oxygen concentration that were more prevalent in polymictic lakes. Specifically, community diversity and amphipod density were generally lower in polymictic lakes. Primary productivity is generally higher in polymictic lakes than in stratified lakes (Fee, 1979; Riley & Prepas, 1985). Polymictic lakes are also typically warmer and more prone to mid-summer diel fluctuation of dissolved oxygen in the littoral zone (Wetzel, 1983) and complete under-ice depletion of dissolved oxygen than stratified lakes (Barica & Mathias, 1979; Babin & Prepas, 1985). These trends illustrate that trophic state and thermal structure may combine to influence the structure of littoral macroinvertebrate communities in lakes on the Boreal Plain.

Dissolved oxygen concentrations of less than 2 mg L^{-1} were recorded at the deep-sites of polymictic lakes, in the same depth range where littoral macroinvertebrates were sampled. Concentrations of dissolved oxygen fluctuate much more widely in the littoral zone than in the pelagic (Wetzel, 1983), increasing the likelihood of even lower concentrations developing during night-respiration periods. Profundal macroinvertebrate biomass (~ 90% Chironomidae and Chaoboridae) is positively related to dissolved oxygen concentrations between 0 and 3 mg L^{-1} in boreal lakes (Dinsmore *et al.*, 1999). Diptera (*e.g.*, Chironomidae) are more tolerant of low dissolved oxygen concentrations than most macroinvertebrates (Nickum, 1970; Davis, 1975; Saether, 1979), and numerically dominated littoral communities in polymictic lakes in my study. Extremely low dissolved oxygen concentrations can contribute to the relative paucity of macroinvertebrates in the littoral zone of shallow, hypertrophic lakes (Takamura & Iwakuma, 1990). I propose that littoral macroinvertebrate communities in eutrophic lakes of low thermal stability may be limited by availability of dissolved oxygen.

This study suggests that littoral macroinvertebrate communities in lakes on the Boreal Plain could be influenced by changes in water-column thermal stability. In north-western Ontario, loss of habitat for cold stenothermic invertebrates has been linked to climatic warming-induced deepening of lake thermoclines (Schindler *et al.*, 1996). *Gammarus* sp., major contributors to community biomass in stratified lakes in the present study, are also cold stenotherms (Smith, 1973) and would likely respond negatively to reduced thermal stability and loss of cold-water habitat. Littoral food webs in lakes that are already shallow and/or weakly thermally stratified are the most likely to be affected by a reduction in thermal stability. LLB800 and LLB20 provide good examples of

systems that would be particularly sensitive to slight reductions in thermal stability, as they were weakly thermally stratified during the study (stability ranged from 5 to 20 g cm cm^{-2}). In addition to affecting invertebrates, thermal regimes also influence the length of the ice-free season, and therefore growing seasons for macrophytes (Wetzel, 1983).

The observed inverse relationship between *Hyallela* sp. and macrophyte biomass lends support to the hypothesis that periodically low dissolved oxygen concentrations in littoral zones negatively affect macroinvertebrate communities. Dense macrophyte beds can impart oxygen stress on littoral macroinvertebrate communities by limiting water circulation during mid-summer-night periods of high phytoplankton and bacterial respiration as well as during late-summer senescence (Wetzel, 1983; Carpenter & Lodge, 1986). The distribution of some mayflies and leeches is determined by the amount of available djssolved oxygen in the littoral zone (Rasmussen, 1988b; Davies & Gates, 1991). It is possible that *Hyallela* sp. are similarly affected by low dissolved oxygen concentrations that can develop in macrophyte beds. Alternatively, the inverse relationship between *Hyallela* sp. biomass and macrophyte biomass could be a result of these organisms inhabiting the canopy of macrophyte beds rather than sediments free of vegetation in lakes with high macrophyte biomass. In some lakes, macroinvertebrate density and biomass is higher in macrophyte beds in comparison to nonvegetated littoral zone sediments (Schramm & Jirka, 1989; Hanson, 1990; Beckett, Aartila & Miller, 1991). Further, macroinvertebrates tend to inhabit macrophyte canopies as opposed to sediments immediately beneath or surrounding macrophyte beds (Hershey, 1985; Rasmussen, 1988a). However, visual inspection of surface waters in macrophyte beds within the polymictic study lakes suggested that *Hyallela* sp. were simply not present. It

is possible that *Hyallela* sp. are inhibited by submerged macrophyte beds and their influence on dissolved oxygen concentration in littoral zones of lakes on the Boreal Plain.

Environmental factors associated with littoral macroinvertebrate communities in lakes on the Boreal Plain are similar to those that determine fish communities throughout boreal regions. Lake depth and associated variables such as temperature and dissolved oxygen concentration determine the distribution of fish species in boreal regions of North America (Tonn & Magnuson, 1982; Robinson & Tonn, 1989; Jackson & Harvey, 1989; Sellers *et al.*, 1997). In my study, thermal stability was associated with the distribution of littoral macroinvertebrates, and polymictic lakes tended to have lower shallow-water dissolved oxygen concentrations than stratified lakes. While shallow lakes (and thus more likely to be polymictic and experience periods of low dissolved oxygen concentration) in north-central Alberta are either fishless or have minnow communities, deeper lakes generally have pike and perch communities (Robinson & Tonn, 1989). Similarly, in my study, macroinvertebrate communities in shallow and polymictic lakes had few or no amphipods, while macroinvertebrate communities in deeper lakes had substantial numbers of amphipods, previously deemed a key food source for pike and perch in lakes on the Boreal Plain (Beaudoin, 1998; Beaudoin *et al.*, 1999). As such, the distribution of littoral macroinvertebrates may also contribute to the distribution of fish among boreal lakes.

Proponents of top-down food web theory maintain that littoral macroinvertebrate community structure is determined, at least in part, by fish predation (*e.g.*, Mittlebach, 1988; Hanson & Butler, 1994). Lakes on the Boreal Plain typically have fewer fish species than lakes in other north temperate regions (Tonn & Magnuson, 1982; Robinson

& Tonn, 1989; Jackson & Harvey, 1989). Assuming that lower numbers of fish species equate to lower predation pressure on macroinvertebrates, relative predation pressure between stratified lakes on the Boreal Plain and north temperate lakes could explain why littoral macroinvertebrate biomass in the former generally exceeded sublittoral macroinvertebrate biomass in the latter (see Fig. 2.2). Top-down theorists would also argue that the spring 1996 winterkill in LLB800 (80-90 % removal of pike and perch) may have resulted in increased density of littoral macroinvertebrates in this lake, relative to lakes that did not experience winterkill. Detailed analysis of LLB800 littoral macroinvertebrate communities suggests that common prey of pike and perch, such as *Gammarus* sp. and *Hyallela* sp., increased in density during the summer immediately after winterkill (see Chapter 3). The influence of predation by fish on littoral macroinvertebrate communities in lakes on the Boreal Plain is unknown, and warrants further investigation.

Sediment organic and water content were not detectably related to littoral macroinvertebrate variables among lakes on the Boreal Plain. Sediment organic content was moderate, and water content was high, and neither varied much among the study lakes. Also, macroinvertebrates were consistently sampled from soft sediments, perhaps minimizing variability in sediment water and organic content between samples both within and among lakes. Littoral slope ranged minimally among the study lakes (0.6 to 5.1%). In contrast, the range in littoral slope was four-fold greater (0.1 to 20 %) and littoral slope proved to be an effective predictor of littoral macroinvertebrate biomass among the north temperate lakes surveyed by Rasmussen & Kalff (1987). Sediment characteristics and littoral slope generally vary widely within a lake, particularly in larger

lakes, and therefore may be better predictors of variation in littoral macroinvertebrate communities within an individual lake (Rasmussen, 1993; Rasmussen & Rowan, 1997).

In summary, this study indicates that littoral macroinvertebrate communities in TP-rich, shallow lakes on the Boreal Plain are negatively associated with TP concentration and positively associated with water-column thermal stability. Further, littoral macroinvertebrate communities may be negatively affected by low dissolved oxygen concentrations that occur in TP-rich, polymictic lakes. Extrapolating my findings, increased trophic state and any shift in water-column thermal structure from stratified to polymictic regimes in lakes on the Boreal Plain could result in decreased taxonomic richness and community diversity within littoral macroinvertebrate communities (Fig. 2.3a). In addition, littoral macroinvertebrate biomass may be positively associated with TP concentration in mesotrophic to eutrophic (*e.g.*, TP concentration range of 20-70 $\mu g\ L^{-1}$) stratified lakes (Fig. 2.3b). However, total littoral macroinvertebrate biomass in polymictic lakes appeared unrelated to TP concentration (Fig. 2.3b). Relative to the communities of stratified lakes, littoral macroinvertebrate communities of TP-rich, polymictic lakes on the Boreal Plain represent less suitable food resources for invertebrate-feeding sportfish such as walleye (*Stizostedion vitreum*), pike, and perch, and some duckling and breeding age waterfowl that can depend on large macroinvertebrates such as amphipods for food (Swanson & Nelson, 1970; Isaak, Neumann & Willis, 1993; Lillie & Evrard, 1994; Beaudoin *et al.*, 1999).

Table 2.1. General physical, geographical, and biological characteristics of the seven study lakes. Surface area, maximum, and mean depth are averages for the two study years. NP=northern pike (*Esox lucius*); YP=yellow perch (*Perca flavescens*); FH=fathead minnow (*Pimephales promelas*); FD=finescale dace (*Phoxinus neogaeus*); BS=brook stickleback(*Culaea inconstans*); WS=white sucker (*Catastomus commersoni*); - indicates pike, perch and white sucker population reduced dramatically by winterkill.

Study Lake	Surface area (ha)[a]	Maximum depth (m)[a]	Mean depth (m)[a]	Location (N,W)[a]	Fish assemblage 1996 Species[b]
LLB20	62	5.6	3.3	55°8', 111°45'	NP, YP
LLB800	104	7.6	2.8	55°12', 111°38'	-
SCL20	56	11	4.8	55°11', 113°39'	FH
SCL800	74	2.9	2.2	55°7', 113°43'	FH,FD,BS
SPH20	157	8.6	4.7	55°25',113°42'	NP,YP,WS
SPH800	65	3.7	2.4	55°22', 113°38'	NP,YP,WS
SPH100	56	2.3	1.4	55°21', 113°43'	BS

Sources: a: E.E. Prepas, unpublished data
b: W. Tonn and A. Danylchuk, unpublished data

Table 2.2. Environmental variables used in Pearson correlation analyses with littoral macroinvertebrate variables. Numbers in parentheses are *S.E.*.

Study Lake	Euphotic [TP] 1996 - 1997 (ug L^{-1})[a]	Thermal stability 1996 - 1997 (g cm cm^{-2})[a]	Macrophyte biomass (g m^{-2})	Sediment Organic content (%)	Sediment water content (%)	Littoral zone slope (%)
LLB20	51 - 49	5 - 8	77 (38)	44 (17)	78 (5)	5.1 (0.8)
LLB800	46 - 55	8 - 20	1.7 (1.7)	31 (5)	68 (16)	2.4 (0.4)
SCL20	51 - 55	80 - 93	5.7 (3.3)	8 (4)	48 (15)	5.1 (0.3)
SCL800	39 - 40	2.7 - 2.3	256 (23)	49 (4)	90 (0.2)	1 (0.1)
SPH20	22 - 26	17 - 32	145 (22)	32 (6)	90 (2)	2.6 (0.4)
SPH800	46 - 38	2.5 - 3.4	58 (18)	54 (2)	92 (1)	3.3 (0.9)
SPH100	100 - 208	0.4 - 3.7	--	--	--	0.6 (0.1)

Sources: a: E.E. Prepas, unpublished data

Table 2.3. Pearson correlations (r) between macroinvertebrate and environmental variables. Amph=amphipoda, Gam=*Gammarus* sp., Hya=*Hyallela* sp., Rich=taxonomic richness, H'=Shannon Wiener index of community diversity. n = 14; * $P < 0.05$; ** $P < 0.01$

	Biomass			Density			Total	
	Amp	Gam	Hya	Amp	Gam	Hya	Rich	H'
TP concentration	--	--	--	--	-0.54*	-0.69*	-0.70**	--
Thermal stability	--	--	--	0.55*	0.55*	0.58*	--	0.72**
Macrophyte biomass	-0.58*	--	-0.63*	--	--	--	--	--
Littoral slope	--	--	--	0.57*	--	0.61*	--	0.55*

Table 2.4. Pearson correlations (r) between littoral macroinvertebrate relative biomass and density and environmental variables.
Dipt=Diptera, Gam=*Gammarus* sp., Hya=*Hyallela* sp.. n = 14; * $P < 0.05$; ** $P < 0.01$.

	Biomass % composition			Density % composition		
	Dipt	Gam	Hya	Dipt	Gam	Hya
TP concentration	0.69**	-0.55*	-0.53*	0.57*	-0.64*	-0.6*
Thermal stability	--	0.71**	0.58*	-0.73**	0.69**	0.53*
Littoral slope	-0.61*	0.56*	--	-0.73**	--	--

Table 2.5. Mean contributions to percent composition of total biomass and density by *Gammarus* sp., Hyallela sp., and Diptera. Numbers in parentheses represent 1 *S.E.*.

		Mean biomass % composition			Mean density % composition		
Lake	Year	*Gammarus* sp.	*Hyallela* sp.	Diptera	*Gammarus* sp.	*Hyallela* sp.	Diptera
Stratified lakes							
SCL20	1996	44 (13)	21 (5)	19 (7)	5 (1)	18 (4)	52 (7)
	1997	24 (9)	11 (8)	14 (9)	3 (1)	11 (4)	40 (14)
SPH20	1996	26 (10)	15 (7)	15 (3)	8 (2)	18 (7)	48 (6)
	1997	30 (8)	19 (2)	7 (1)	13 (3)	33 (4)	26 (8)
LLB800	1996	15 (5)	42 (3)	15 (3)	2 (1)	43 (6)	47 (7)
	1997	12 (5)	14 (7)	14 (2)	4 (2)	13 (5)	41 (4)
LLB20	1996	8 (5)	10 (4)	20 (10)	3 (1)	13 (9)	47 (12)
	1997	3 (3)	2 (2)	32 (9)	0.4 (0.4)	1 (1)	37 (3)
Polymictic lakes							
SPH800	1996	0 (0)	0 (0)	37 (10)	0 (0)	0 (0)	81 (2)
	1997	23 (8)	11 (7)	19 (7)	2 (1)	6 (3)	73 (6)
SCL800	1996	10 (7)	16 (11)	26 (11)	6 (6)	13 (7)	59 (10)
	1997	0 (0)	0 (0)	52 (7)	6 (6)	13 (7)	59 (10)
SPH100	1996	0 (0)	0 (0)	51 (10)	0 (0)	0 (0)	91 (3)
	1997	0 (0)	0 (0)	94 (1)	0 (0)	0 (0)	95 (1)

Table 2.6a. Percent similarity indexes across the decreasing thermal stability gradient.

1996	SCL20	SPH20	LLB800	LLB20	SCL800	SPH800	SPH100
SCL20	1	0.80	0.78	0.78	0.78	0.59	0.55
SPH20		1	0.78	0.65	0.76	0.59	0.54
LLB800			1	0.61	0.75	0.57	0.55
LLB20				1	0.60	0.46	0.44
SCL800					1	0.69	0.67
SPH800						1	0.85
SPH100							1

Table 2.6b. Percent similarity indexes across the decreasing thermal stability gradient.

1997	SCL20	SPH20	LLB800	LLB20	SPH800	SPH100	SCL800
SCL20	1.000	0.65	0.76	0.53	0.61	0.21	0.49
SPH20		1.000	0.77	0.60	0.52	0.22	0.40
LLB800			1.000	0.60	0.59	0.26	0.50
LLB20				1.000	0.46	0.22	0.45
SPH800					1.000	0.22	0.87
SPH100						1.000	0.24
SCL800							1.000

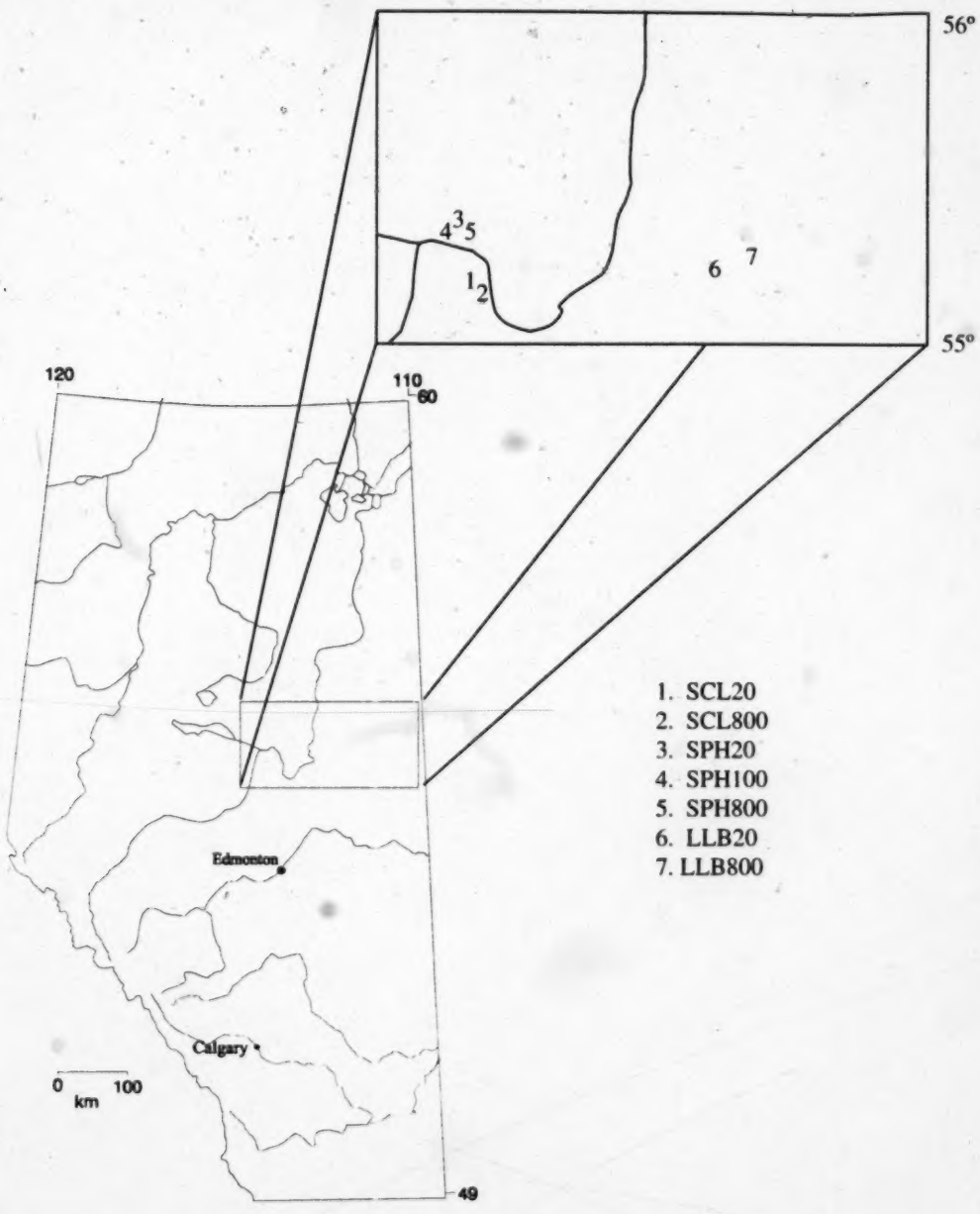

Figure 2.1: Alberta map showing the location of the study lakes.

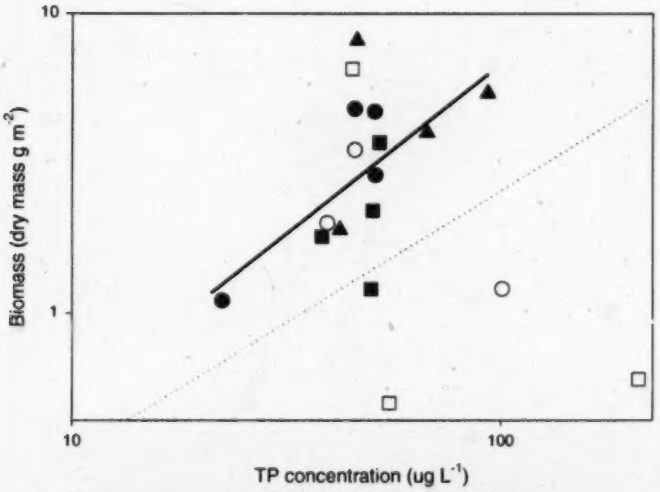

Figure 2.2. Plot of littoral macroinvertebrate dry mass biomass on mean summer total phosphorus (TP) concentration. Filled points are from stratified lakes, open points are from polymictic lakes. Circles are from TROLS lakes (1996), squares from TROLS lakes (1997), triangles from Yee (1997). Solid LS regression line for all points from stratified lakes. Dotted line is re-created from relationship between sublittoral macroinvertebrate biomass and TP concentration from Rasmussen and Kalff (1987).

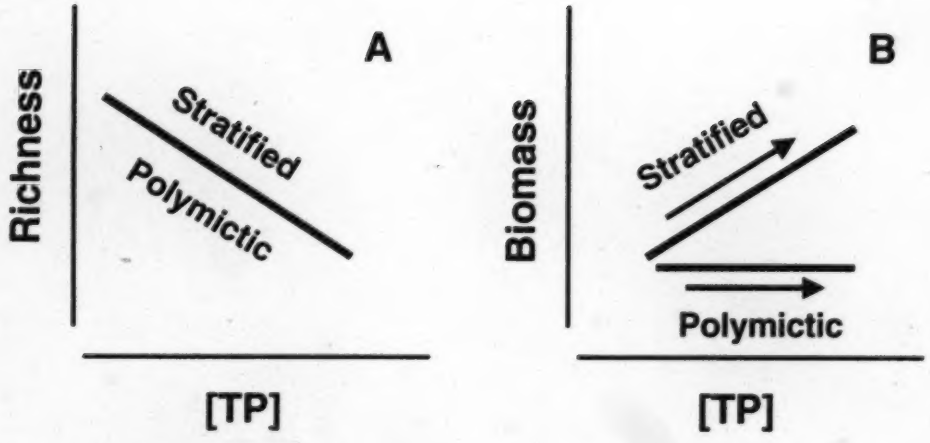

Figure 2.3. Schematic trends illustrating associations between (A) taxonomic richness and (B) total community biomass with trophic state in Boreal Plain lake littoral macroinvertebrate communities.

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Chapter 3
RESPONSE TO WINTERKILL IN A LITTORAL MACROINVERTEBRATE COMMUNITY

3.1 Introduction

Littoral macroinvertebrates represent an important source of food to fish (Jónasson, 1978; Mittlebach, 1988). The density of organisms lower in the food web can be affected through top-down cascading effects of fish predation (Carpenter, Kitchell & Hodgson, 1985; Carpenter *et al.*, 1987; Carpenter & Kitchell, 1988). However, the relationship between littoral macroinvertebrate density and predatory fish under natural conditions remains poorly quantified.

Numerous experiments designed to test the effect of fish predation on macroinvertebrate density have produced conflicting results. Fish removals, introductions, and comparisons between lakes with and without fish suggest that macroinvertebrate density is inversely related to fish predation (Ball & Hayne, 1952; Post & Cucin, 1984; Dermott, 1988; Hanson & Butler, 1994). In contrast, direct manipulations of fish and macroinvertebrate densities in experimental mesocosms suggest that macroinvertebrate density is either variably (*e.g.*, Crowder & Cooper, 1982; Mittlebach, 1988) or minimally (*e.g.*, Thorp & Bergey, 1981a; 1981b; Pierce & Hinrichs, 1997; Cobb & Watzin, 1998) impacted by fish predation. Other mesocosm-level studies have concluded that macroinvertebrate response to fish predation is moderated by substrate heterogeneity (Gilinsky, 1984; Diehl, 1992). Simultaneous observation of littoral macroinvertebrate and benthivorous fish densities over time in lakes in which fish density can vary dramatically between years would provide valuable insight regarding the importance of fish in structuring littoral macroinvertebrate communities.

Winterkill is a natural phenomenon that selectively culls large-bodied individuals from fish assemblages and thus has the potential to dramatically reduce predation pressure (Casselman & Harvey, 1975; Tonn & Paszkowski, 1986). Shallow, productive lakes, such as those in north-central Alberta, are prone to depletion of dissolved oxygen and winterkill (Tonn & Magnuson, 1982; Babin & Prepas, 1985). Lakes of this region are typically dominated by one of two distinct fish assemblage types; shallower lakes are generally characterized by small-bodied fish such as fathead minnows (*Pimephales promelas*) and brook stickleback (*Culaea inconstans*), and deeper lakes are generally characterized by large-bodied fish, including northern pike (*Esox lucius*) and yellow perch (*Perca flavescens*) (Robinson & Tonn, 1989). Small-bodied fish consume primarily chironomid larvae (Price, Tonn & Paszkowski, 1991), whereas larger-bodied fish prey primarily upon larger invertebrates, including *Gammarus* sp., *Hyallela* sp., chironomids, and chaoborid larvae, and less frequently on other taxa, including hirudineans (leeches), sphaerid clams, and trichopteran and ceratopogonid larvae (Beaudoin, 1998; Beaudoin *et al.*, 1999). If predation by fish is an important mechanism limiting macroinvertebrate populations, alleviation of predation pressure via winterkill should result in an increase in the density of common macroinvertebrate prey taxa.

The opportunity to study the effects of winterkill on benthic food webs arose serendipitously during a study of macroinvertebrate community structure in lakes on the Boreal Plain (see Chapter 2). The primary objective of the research summarized in this chapter was to quantify the response of littoral macroinvertebrate density to a dramatic reduction in predatory pike and perch density followed by gradual recovery of the fish assemblage. To place these observations into perspective, the macroinvertebrate

communities of three other lakes with pike and perch assemblages were sampled: one lake over an identical time frame to the winterkill lake, and two lakes over a portion of the same time frame. Severe winterkill was not documented in any of the three 'reference' lakes, but total fish density varied over time nonetheless. The second objective was to determine if changes in predation pressure, such as those caused by winterkill, resulted in changes in the absolute density and relative density (percent composition) structure of macroinvertebrate communities. I hypothesized that, for littoral taxa that are common prey of pike and perch, a reduction in predation pressure (fish density) would result in an increase in absolute and relative macroinvertebrate density, and conversely, that an increase in predation pressure would result in a decrease in absolute and relative macroinvertebrate density.

3.2 Materials and Methods

Macroinvertebrate samples were collected from LLB800 and SPH20 in mid-summer of 1995 (I), 1996 (II), and 1997 (III), and from SPH800 and LLB20 in 1996 (II) and 1997 (III). Four Ekman dredge samples were collected from mid-littoral zone sediments (1.5 to 3 m depth) in LLB800 and SPH20 during period I. Six samples per lake were collected during the remaining sampling periods. Grab contents were sieved in the field through a 200-µm Nitex bag and preserved in 4 % formalin solution. In the laboratory, samples were sieved through 1-mm mesh to separate macroinvertebrates from sediments. Macroinvertebrates were picked under low power dissecting microscope and identified following keys by Clifford (1991). Macroinvertebrate sampling and the study lakes are described in further detail in Chapter Two.

With the exception of LLB800 in 1997, when fish were collected by W. Tonn (Unpublished data), all fish data are from W. Tonn & A. Danylchuk (Unpublished data). The winterkill in LLB800 occurred in the spring of 1996 and removed 80 to 90% of the pike and perch assemblage. In addition, fish were collected from SPH20, SPH800, and LLB20, lakes with pike and perch that did not experience severe winterkill during the study. Fish were collected via overnight sets of Lundgren multi-mesh survey gillnets (42 x 1.5 m, with fourteen 3-m wide panels of 6.25-75 mm bar mesh) during summers of 1995 (I), 1996 (II), and 1998 (IV), with total fishing effort adjusted for lake size (area, depth). For the purpose of comparing changes in fish density over time with changes in macroinvertebrate density over time, it was assumed that 1997 fish densities were equivalent to those recorded in 1998.

I hypothesized that fish predation influences the macroinvertebrates most commonly eaten by pike and perch by consistently depressing the density of large individuals. By this reasoning, the density of common macroinvertebrate prey taxa should increase when fish density is reduced by winterkill. Congruently, the density of common macroinvertebrate prey taxa should decrease when fish density increases in a given lake. Macroinvertebrate and fish densities were compared between sampling periods by Mann-Whitney *U*, this test being robust to non-normality and small and unequal sample sizes. The relative contribution of each macroinvertebrate taxon to total macroinvertebrate density was also compared between sampling periods by Mann-Whitney *U*.

3.3 Results

Fish density

Patterns in fish density differed over time in three of four study lakes (Table 3.1). Total fish catch in LLB800 decreased from over 3 fish h^{-1} in 1995 to 0 fish h^{-1} in 1996 following the winterkill, and increased to 0.6 fish h^{-1} in 1998 (Table 3.1, Fig. 3.1). Survey of the LLB800 fish assemblage in 1997 suggested that the population was already beginning to recover from the 1996 winterkill. In contrast, over the same time period in SPH20, total fish catch increased three-fold from 1 to 3.5 fish h^{-1} between 1995 and 1996, and decreased by 50 % to 1.8 fish h^{-1} between 1996 and 1998 sampling periods (Fig. 3.2). Total fish community catch-per-hour in SPH20 differed between sampling periods over time, but 1995 and 1998 catches were not detectably different from one another (Table 3.1, Fig. 3.2). In SPH800, fish density decreased dramatically from 3 fish h^{-1} in 1996 to 0.13 fish h^{-1} in 1998 (Table 3.1, Fig. 3.3). In contrast to the previously mentioned lakes, fish density in LLB20 was not detectably different between 1996 (0.86 fish h^{-1}) and 1998 (0.11 fish h^{-1}) sampling periods (Table 3.1, Figure 3.4). The between year variability in measured and projected fish density among the study lakes provided appropriate conditions under which to test the effects of year-to-year changes in fish density on the density of macroinvertebrates that are common prey of fish.

Macroinvertebrate density

When fish density decreased or was projected to have decreased between sampling periods in LLB800, SPH20, and SPH800, the density of several macroinvertebrate taxa increased. When LLB800 experienced winterkill between 1995 and 1996, *Gammarus* sp.

and hirudinean densities increased eight and ten fold, respectively (Table 3.2, Fig. 3.1). *Hyallela* sp. and chironomid ($z = -1.8$, $P = 0.07$) densities also increased two and seven fold, respectively, however, differences between 1995 and 1996 for these taxa were not significant (Table 3.2, Fig. 3.1). Chaoborid, ceratopogonid, and trichopteran density decreases between 1995 and 1996 were not measurable in LLB800 (Table 3.2, Fig. 3.1). In SPH800, *Gammarus* sp., *Hyallela* sp., hirudinean, ceratopogonid, and sphaerid clam densities all increased between 1996 and 1997, the same period over which fish density presumably decreased (Table 3.3, Fig. 3.3). The direction of change in chironomid and chaoborid densities was also positive between 1996 and 1997 in SPH800, however differences between years were not significant (Table 3.3, Fig. 3.3). Trichopteran density was not measurably different between 1996 and 1997 in SPH800 (Table 3.3, Fig. 3.3). Fish density presumably decreased in SPH20 between 1996 and 1997 (Fig. 3.2). Over the same time period, *Hyallela* sp. density increased three fold (Table 3.4, Fig. 3.2). The direction of change in density of *Gammarus* sp., Hirudinea, and sphaerid clams was also positive between 1996 and 1997 in SPH20 (Fig. 3.2), however, differences in density of these taxa, as well as of chironomids, chaoborids, trichopterans, and ceratopogonids, were not significant (Table 3.4). Thus, when fish density decreased in a lake, the density of large macroinvertebrates, such as *Gammarus* sp. and *Hyallela* sp., tended to increase.

Conversely, when fish density increased between sampling periods in a lake, the density of some macroinvertebrates decreased. In LLB800, fish were recovering from the 1996 winterkill when sampled in 1997 and 1998, and *Hyallela* sp. density decreased by 80 % between 1996 and 1997 (Table 3.2, Fig. 3.1). The direction of change in *Gammarus* sp., chironomid ($z = -1.9$, $P = 0.07$), trichopteran, and ceratopogonid densities

was also negative between 1996 and 1997, however, as for hirudineans and sphaerid clams, differences in density between these sampling periods were not significant (Table 3.2). Chaoborid densities increased from 0 to 700 m^{-2} between 1996 and 1997 in LLB800 (Table 3.2, Fig. 3.1). While fish density increased in SPH20 between 1995 and 1996, *Hyallela* sp. density decreased approximately nine-fold (Table 3.4, Fig. 3.2). Although differences in density of the remaining macroinvertebrate taxa were not significant in SPH20, the direction of change in *Gammarus* sp., chironomid, hirudinean, trichopteran, and sphaerid clam density between 1995 and 1996 was also negative (Table 3.4, Fig. 3.2). When fish density increased over time in LLB800 and SPH20, *Hyallela* sp. density decreased significantly, and the direction of change in *Gammarus* sp. was also negative.

LLB20 was the lone study lake in which fish density presumably did not change between sampling periods. Interestingly, this was also the only study lake where the density of all eight macroinvertebrate taxa examined did not detectably differ between sampling periods (Table 3.5, Fig. 3.4).

To generalize across the study lakes, 10 of 11 significant differences detected in macroinvertebrate density between successive sampling periods were in an opposite direction to the corresponding or projected change in fish density. Nine of these ten measurable and opposite differences were observed in LLB800 and SPH800. When measured in mid-September, 1997, LLB800 (1.7 ± 1.7 dry mass g m^{-2}) had low submerged macrophyte biomass, SPH800 (58 ± 18 dry mass g m^{-2}) and LLB20 (77 ± 38 dry mass g m^{-2}) had moderate submerged macrophyte biomass, and SPH20 (145 ± 22 dry mass g m^{-2}) had high submerged macrophyte biomass (Chapter 2). Six of the ten

measurable and opposite differences were for either *Gammarus* sp. or *Hyallela* sp. (amphipods). In all 10 cases where fish density differed or was projected to have differed (five for each taxa examined), the direction of change in amphipod (*Gammarus* sp. and *Hyallela* sp.) density was opposite to that of fish. In six of these ten instances, changes in amphipod density were detectable. Overall, when fish density was different between successive sampling periods, 27 of 40 changes in macroinvertebrate density were in the opposite direction. These results suggest that macroinvertebrate density, especially amphipod density, may be influenced by year-to-year changes in predatory pike and perch density.

Macroinvertebrate relative density

The trends for year-to-year change in macroinvertebrate relative density were similar to those reported for regular density in relation to increased, decreased, and unchanged (either measured or projected) fish density. In LLB800, when fish density decreased between 1995 and 1996, *Gammarus* sp. and hirudinean relative densities increased by 4.4 and 0.4 %, respectively (Table 3.6). In addition, sphaerid relative density decreased by 6.2 % between 1995 and 1996 in LLB800. While fish density presumably decreased between 1996 and 1997 in SPH20, the relative density of *Hyallela* sp. increased 2.5 fold, and that of chironomids decreased 3.5 fold (Table 3.7). When fish density presumably decreased between 1996 and 1997 in SPH800, the relative density of *Gammarus* sp, (3.3 %) *Hyallela* sp. (6.8 %), and hirudinea (1.1 %) all increased (Table 3.8).

Where fish density increased between sampling periods, changes in macroinvertebrate relative density were similar to the changes in absolute density.

Between 1996 and 1997 in LLB800, relative density of *Hyallela* sp. decreased from 62 to 27 % (Table 3.6). However, in contrast to the trends of no change observed for regular density, relative densities of Chaoboridae, Hirudinea, and Sphaeridae all increased significantly (Table 3.6), perhaps due in part to the large decrease in *Hyallela* sp. density (Table 3.2). In SPH20, *Hyallela* sp. relative density increased markedly from 58 to 17 % between 1995 and 1996 (Table 3.8). Between the same sampling periods, chironomid relative density increased from 19 to 38 % (Table 3.8). For all macroinvertebrate taxa examined in LLB20, relative density did not detectably differ between 1996 and 1997 (Table 3.9).

Similarly to, but not as consistently as for regular density, the relative density of amphipods tended to vary inversely to measured or projected fish density among the study lakes. However, large changes in density of a given macroinvertebrate taxon likely contributed to opposite changes in relative density of other taxa for which density did not actually change over time.

3.4 Discussion

The density of macroinvertebrates that are common prey of pike and perch, such as *Gammarus* sp. and *Hyallela* sp., was inversely related to fish density in all four study lakes. The density of other macroinvertebrates, some common prey, and others less common prey of pike and perch (*e.g.*, leeches, trichopterans, ceratopogonids and sphaerids, chironomids, chaoborids), was not consistently related to measured or projected fish density. These observations suggest that pike and perch may directly

contribute to the structure of littoral macroinvertebrate communities by reducing the density of larger, common prey taxa.

Studies of whole-lake fish removal and introduction, as well as some mesocosm-level experiments, suggest that littoral macroinvertebrate density is affected by fish predation. The density dynamics of *Hyallela* sp., *Gammarus* sp., chironomid and chaoborids observed following winterkill in LLB800 and after reduction of fish density in SPH800 and SPH20 parallel the results of fish removal experiments, wherein total macroinvertebrate density (Ball & Hayne, 1952) and amphipod (first summer), chironomid, and chaoborid (second summer) density (Hanson & Butler, 1994) increased following rotenone treatment. Macroinvertebrate community biomass had decreased by 50% when measured 12 years following yellow perch introduction to a central Ontario lake (Post & Cucin, 1984). Through pond and *in situ* mesocosm experiments, researchers have concluded that higher predation pressure removes large macroinvertebrates from the community, shifting size structure to dominance by smaller individuals (*e.g.*, Crowder & Cooper, 1982; Mittlebach, 1988). My observations support the theory that the density of large, common macroinvertebrate prey, may be influenced by predation by pike and perch.

Collection of observations pre- and post-winterkill has key similarities and differences with whole-lake fish removals or introductions. Winterkill, like fish removal or introduction (*e.g.*, Ball & Hayne, 1952; Post & Cucin, 1984; Hanson & Butler, 1994), is a rapid change in food web structure and predation pressure. While the direct effect of low under-ice dissolved oxygen concentration on macroinvertebrate survivorship was not investigated in my study, high mortality of chaoborid, leech, and odonate nymphs was

observed by Ball & Hayne (1952) after rotenone treatment. In addition, fish were removed from treated lakes following poisoning (*e.g.*, Ball & Hayne, 1952; Hanson & Butler, 1994), whereas after winterkill in my study, carcasses were left to decompose on the lake bottom. Fish carcasses are likely to contribute to benthic food webs by providing fresh nutrients and organic matter for scavenging macroinvertebrates (Wipfli, Hudson & Caouette, 1998). Thus, despite similarities in results, parallels between the observations made in my study and the results of fish removal and introduction experiments must be drawn with caution.

In contrast to fish removal and introduction experiments, several pond and mesocosm experiments suggest that macroinvertebrate density and fish predation are not tightly linked. Macroinvertebrate density and biomass in experimental ponds of different fish density were variable, but did not appear to be related to fish predation (Butler, 1989; Pierce & Hinrichs, 1997; Cobb & Watzin, 1998). Macroinvertebrate density did not differ when fish exclusion and control plots were compared in Par Pond, North Carolina (Thorp & Bergey, 1981a; 1981b). In these studies, low correlation between fish and macroinvertebrate density was attributed to the confounding effects of habitat structural complexity created by macrophytes in experimental ponds, as demonstrated by Gilinsky (1984) and Diehl (1992). Submerged macrophyte biomass was lowest in LLB800, moderate in SPH800 and LLB20, and highest in SPH20. Assuming that higher macrophyte biomass hinders fish feeding success in littoral habitats, relative macrophyte biomass may account for differences in macroinvertebrate response to changes in fish density among the study lakes.

The timing of response to a change in fish density is likely linked to the life cycle characteristics of a given macroinvertebrate taxon. In boreal lakes, *Gammarus* sp. and *Hyallela* sp. are sexually mature at ice-out in spring, and mate shortly thereafter, with young-of-the-year hatching approximately three weeks later and maturing over the course of the summer (Clifford, 1991; Wen, 1992). Amphipods are thus well-suited to take advantage of winterkill-related reductions in fish density, as loss of breeding adults to fish predation is reduced by the reduction in fish density, and the new cohort is introduced to 'predation-reduced' conditions shortly after the loss of fish. Dipteran density and fish density were not consistently inversely related across the study lakes. However, if dipteran density was negatively influenced by predation by fish, the observed changes in dipteran density over time in LLB800 might have been expected. Chironomids in Alberta lakes are typically uni- or multi-voltine (Clifford, 1991), and thus would be likely to exhibit a relatively short response time to reduced predation pressure, as the benefits of lowered predation pressure work through the food web in subsequent generations. Larval chaoborids generally complete one life cycle per year and pupate and emerge early each summer (Merritt & Cummins, 1984; Clifford, 1991). Since late-instar larvae and pupae would only have been exposed to reduced fish density for a short period of time prior to emergence in 1996, the benefits of such a reduction would not have taken the form of increased larval density until the summer following winterkill, as observed in LLB800. Thus, general life-history characteristics of the macroinvertebrates that are common pike and perch prey further imply that observed changes in density post-winterkill might be due in part to reduced predation pressure.

It was hypothesized post-hoc that the increase in chaoborid density observed

16 mo following winterkill in LLB800 may have been in part due to colonization by *Chaoborus americanus*, the dipteran larva that lives primarily in fishless lakes (von Ende, 1979; Lamontagne & Schindler, 1994). Two simultaneous studies in LLB800 resulted in collection of chaoborids: from littoral sediments in my study, and from the pelagic zone by B. Pinel-Alloul, G. Méthot & C. Bouffard (Unpublished data). Chaoborids collected from littoral sediments in LLB800 and identified to species for 1995 and 1997 were *C. flavicans*. No chaoborids were detected in pelagic zooplankton samples from LLB800 in 1995, while in 1996 and 1997, chaoborids were present, further suggesting that these organisms may have benefited under reduced predation pressure. No *C. Americanus* were found in 1996 and 1997 pelagic zooplankton samples (B. Pinel-Alloul, G. Méthot & C. Bouffard, unpublished data). Similar to the observed increase in chaoborid density in LLB800, the density of *C. punctipennis* increased substantially after fish density reduction in Tuesday Lake, Michigan (Elser *et al.*, 1987). *C. flavicans* and *C. punctipennis* are known to co-exist with fish, but are vulnerable prey and likely to benefit in the absence of predation by fish.

My observation that amphipod density may be inversely related to pike and perch density indicates that amphipods would be appropriate target organisms for future study of lake food web dynamics. In chapter two, amphipods were more prevalent in deeper, nutrient-poor lakes, relative to shallower, nutrient-rich lakes, perhaps due to sensitivity to low dissolved oxygen concentrations in the latter. Previous research has shown that amphipods can be particularly sensitive to changes in physical habitat, including temperature and pH (Smith, 1973; Stephenson & Mackie, 1986; Yee, 1997). Thus, in any given lake, presence and density of amphipods are likely related to a suite of

biogeochemical factors. As such, amphipods would be valuable study organisms in determining the relative importance of top-down and bottom-up processes in lake food webs.

Amphipods are also highly mobile organisms, and can be found burrowing into sediments, darting in and out of macrophyte over-story, or swimming in the open water of lakes on the Boreal Plain. Researchers seeking to measure year-to-year fluctuations in amphipod density could increase their accuracy by accounting for this mobility and any potential trap-avoidance behaviours in their sampling protocol. Distributing samples among the different habitats that amphipods utilize and increasing the number of samples collected would likely provide results more representative of whole-lake trends.

This study suggests that the density of large, common prey of pike and perch, in particular the amphipods *Gammarus* sp. and *Hyallela* sp., may be influenced by pike and perch predation in lakes on the Boreal Plain of Alberta. Specifically, macroinvertebrates in sparsely vegetated lakes that experienced large reductions in fish density through winterkill or other natural processes, appeared to respond more than macroinvertebrates in more densely vegetated lakes in which fish density varied from year-to-year, but did not experience severe winterkill. Longer term simultaneous collection of pike and perch and macroinvertebrates would improve our understanding of the possible relationship between predatory fish density and the density of their common macroinvertebrate prey. Littoral macroinvertebrate taxa that are preyed upon less frequently by pike and perch, such as sphaerid clams, trichopterans, and ceratopogonids, accordingly did not appear to be consistently affected by changes in fish density. Pike and perch may contribute to the

structure of littoral macroinvertebrate communities in lakes on the Boreal Plain, in particular to the density of larger, common prey.

Table 3.1. Results of Mann Whitney *U* tests of change in catch-per-unit-effort (total fish assemblage catch-per-hour) between sampling periods in four north-central Alberta lakes.
Delta median is the change in catch-per-unit-effort between sampling periods. Significant differences ($P < 0.05$) are printed in bold.

	1995 - 96			1996 - 98			1995 - 98		
Lake	Delta Median	*z*	*P*	Delta Median	*z*	*P*	Delta Median	*z*	*P*
LLB800	-3.24	-3.2	**0.001**	0.51	-3.2	**0.001**	-2.73	-3.8	**0.001**
SPH20	1.49	-3.8	**0.001**	-1.25	-2.3	**0.02**	0.24	-0.2	-0.86
SPH800	--	--	--	-2.89	-3.4	**0.001**	--	--	--
LLB20	--	--	--	-0.75	-1.2	0.26	--	--	--

Table 3.2. Results of Mann Whitney *U* tests of change in littoral macroinvertebrate density between sampling periods in LLB800 (Winterkill and gradual recovery of fish assemblage). Delta median is the change in median macroinvertebrate density (m-2) between sampling periods. Significant differences ($P < 0.05$) are printed in bold.

		1995 - 96			1996 - 97			1995 - 97		
Lake	Taxon	Delta median	*z*	*P*	Delta median	*z*	*P*	Delta median	*z*	*P*
LLB800	*Gammarus* sp.	1616	-2.1	**0.04**	-1078	-1.8	0.09	539	-1.8	0.07
	Hyallela sp.	17649	-0.9	0.48	-21033	-2.4	**0.02**	-3383	-1.5	0.17
	Chironomidae	7262	-1.8	0.07	-7047	-1.9	0.07	216	0	0.76
	Chaoboridae	-22	-1.2	0.35	582	-3	**0.002**	560	-2.6	**0.01**
	Hirudinea	129	-2.1	**0.04**	151	-1.8	0.09	280	-2.6	**0.01**
	Trichoptera	-151	-1.5	0.17	-65	-1.6	0.18	-216	-1.8	0.11
	Ceratopogonidae	-302	-0.9	-0.48	-840	-1.8	0.09	-1142	-2	0.07
	Sphaeridae	-237	-1.1	0.35	129	-0.6	0.59	-108	-0.5	0.61

Table 3.3. Results of Mann Whitney *U* tests of change in littoral macroinvertebrate density between sampling periods in SPH800 (Projected decrease in fish density). Delta median is the change in median macroinvertebrate density (m^{-2}) between sampling periods.
density (m^{-2}) between sampling periods. Significant differences ($P < 0.05$) are printed in bold.

		1996 - 97		
		Delta		
Lake	Taxon	median	*z*	*P*
SPH800	*Gammarus* sp.	603	-3.1	**0.002**
	Hyallela sp.	1293	-2.9	**0.002**
	Chironomidae	4978	-0.8	0.49
	Chaoboridae	22	-1.9	0.18
	Hirudinea	431	-3.1	**0.002**
	Trichoptera	0	-1.5	0.39
	Ceratopogonidae	302	-2.4	**0.02**
	Sphaeridae	3771	-2.4	**0.02**

Table 3.4. Results of Mann Whitney *U* tests of change in littoral macroinvertebrate density between sampling periods in SPH20 (Measured increase, projected decrease in fish density).
Delta median is the change in median macroinvertebrate density (m^{-2}) between sampling periods. Significant differences ($P < 0.05$) are printed in bold.

		1995 - 96			1996 - 97			1995 - 97		
Lake	Taxon	Delta median	*z*	*P*	Delta median	*z*	*P*	Delta median	*z*	*P*
SPH20	*Gammarus* sp.	-65	-0.6	0.61	539	-1.5	0.13	474	-0.6	0.61
	Hyallela sp.	-9116	-2.6	**0.01**	2414	-2.2	**0.03**	-6702	-2.3	**0.02**
	Chironomidae	-668	-1.7	0.07	-1034	-1.6	0.13	-1702	-2.6	**0.01**
	Chaoboridae	86	-1.9	0.11	-86	-1.8	0.09	0	-0.3	0.91
	Hirudinea	-43	-0.9	0.48	65	-0.3	0.82	22	-0.2	0.91
	Trichoptera	-86	-0.5	0.61	-65	-1.3	0.24	-151	-1.7	0.11
	Ceratopogonidae	43	-1	0.35	-22	-0.6	0.59	22	-0.5	0.76
	Sphaeridae	-323	-1.2	0.26	65	-0.1	0.94	-259	-0.3	0.76

Table 3.5. Results of Mann Whitney *U* tests of change in littoral macroinvertebrate density between sampling periods in LLB20 (Projected no change in fish density). Delta median is the change in median macroinvertebrate density (m-2) between sampling periods. Significant differences ($P < 0.05$) are printed in bold.

		1996 - 97		
Lake	Taxon	Delta median	*z*	*P*
LLB20	*Gammarus* sp.	-453	-1.4	0.24
	Hyallela sp.	-927	-1.7	0.09
	Chironomidae	2823	-1.6	0.13
	Chaoboridae	22	-0.8	0.48
	Hirudinea	-22	-0.4	0.82
	Trichoptera	-43	-1.8	0.13
	Ceratopogonidae	0	-0.2	0.94
	Sphaeridae	-22	-0.3	0.82

Table 3.6. Results of Mann Whitney *U* tests of change in relative density of littoral macroinvertebrates between sampling periods in LLB800 (Winterkill and gradual recovery of the fish assemblage).
Delta median is the change in median % composition between sampling periods. Significant differences ($P < 0.05$) are printed in bold.

		1995 - 96			1996 - 97			1995 - 97		
Lake	Taxon	Delta median	*z*	*P*	Delta median	*z*	*P*	Delta median	*z*	*P*
LLB800	*Gammarus* sp.	4.4	-2.1	**0.04**	2.6	-1.4	0.39	7.0	-2.6	**0.02**
	Hyallela sp.	18.0	-1.3	0.26	-35.0	-2.9	**0.002**	-17.3	-1.5	0.48
	Chironomidae	16.2	-1.3	0.26	-3.4	-0.2	0.94	12.7	-1.5	0.17
	Chaoboridae	-0.1	-1.3	0.35	10.0	-3.0	**0.002**	10.0	-2.6	**0.02**
	Hirudinea	0.4	-2.1	**0.04**	2.9	-2.1	**0.04**	3.3	-2.6	**0.01**
	Trichoptera	-2.8	-1.5	0.17	-0.2	-0.9	0.49	-2.9	-1.8	0.11
	Ceratopogonidae	-11.3	-0.9	0.48	-1.3	-0.5	0.70	-12.5	-1.5	0.17
	Sphaeridae	-6.2	-2.6	**0.01**	9.0	-2.9	**0.002**	2.8	-0.9	0.48

Table 3.7. Results of Mann Whitney *U* tests of change in relative density of littoral macroinvertebrates between sampling periods in SPH20 (Measured increase and projected decrease in fish density). Delta median is the change in median % composition between sampling periods.
Significant differences ($P < 0.05$) are printed in bold.

		1995 - 96			1996 - 97			1995 - 97		
Lake	Taxon	Delta median	*z*	*P*	Delta median	*z*	*P*	Delta median	*z*	*P*
SPH20	*Gammarus* sp.	11.4	-1.3	0.26	1.0	-0.5	0.70	12.4	-1.7	0.11
	Hyallela sp.	-40.9	-2.6	**0.01**	29.4	-2.4	**0.02**	-11.5	-1.9	0.07
	Chironomidae	18.6	-2.3	**0.02**	-26.4	-2.9	**0.002**	-7.9	-1.5	0.17
	Chaoboridae	1.8	-1.7	0.11	-1.8	-1.9	0.07	0.0	-0.3	0.91
	Hirudinea	0.8	-1.7	0.17	-0.3	-1.0	0.82	1.1	-0.9	0.48
	Trichoptera	1.1	-0.5	0.61	-1.9	-1.9	0.07	-0.9	-1.0	0.35
	Ceratopogonidae	0.9	-1.4	0.26	-0.6	-1.1	0.31	0.3	-0.8	0.48
	Sphaeridae	5.5	-1.9	0.11	-3.3	-1.0	0.70	2.1	-0.4	0.76

Table 3.8. Results of Mann Whitney *U* tests of change in relative density of littoral macroinvertebrates between sampling periods in SPH800 (Projected decrease in fish density). Delta median is the change in median % composition between sampling periods. Significant differences ($P < 0.05$) are printed in bold.

		1996 - 97		
		Delta		
Lake	Taxon	median	*z*	*P*
SPH800	*Gammarus* sp.	3.3	-3.1	**0.002**
	Hyallela sp.	6.8	-2.3	**0.03**
	Chironomidae	-22.0	-1.9	0.07
	Chaoboridae	0.1	-1.9	0.18
	Hirudinea	1.1	-3.1	**0.002**
	Trichoptera	0	-1.5	0.39
	Ceratopogonidae	0.5	-0.8	0.48
	Sphaeridae	6.1	-0.8	0.48

Table 3.9. Results of Mann Whitney *U* tests of change in relative density of littoral macroinvertebrates between sampling periods in LLB20 (Projected no change in fish density). Delta median is the change in median % composition between sampling periods. Significant differences ($P < 0.05$) are printed in bold.

		1996 - 97		
		Delta		
Lake	Taxon	median	*z*	*P*
LLB20	*Gammarus* sp.	-3.5	-1.4	0.24
	Hyallela sp.	-5.4	-1.7	0.09
	Chironomidae	21.9	-1.1	0.31
	Chaoboridae	0.1	-0.5	0.70
	Hirudinea	-0.1	-0.2	0.94
	Trichoptera	-0.4	-0.1	0.18
	Ceratopogonidae	0.0	-0.4	0.82
	Sphaeridae	1.4	-0.2	0.94

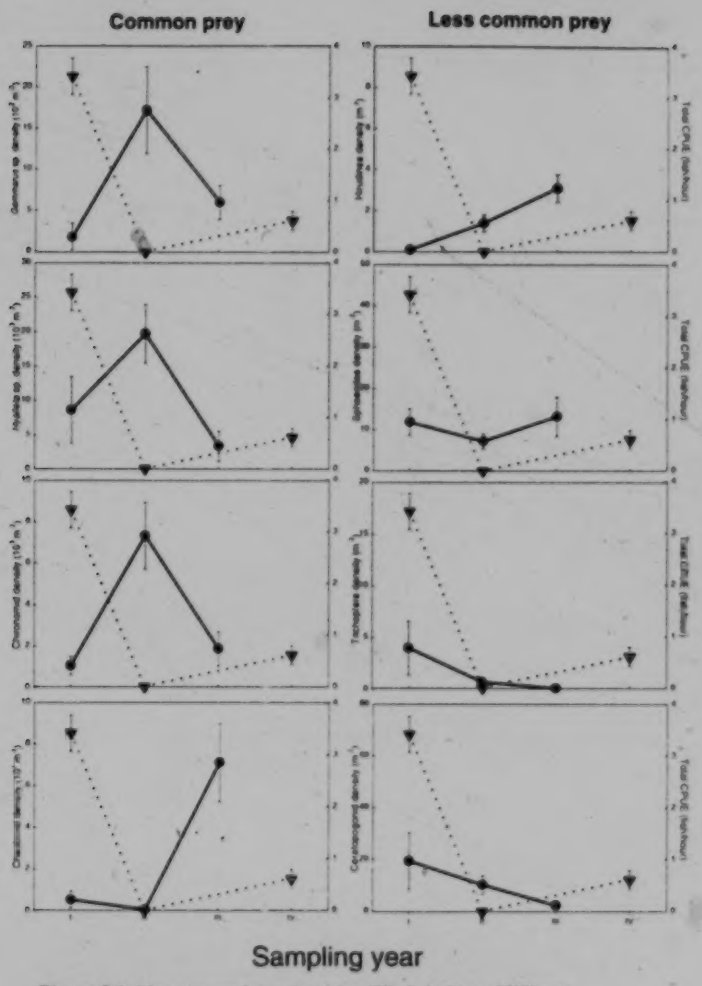

Figure 3.1. Macroinvertebrate densities (filled circles, solid lines) and total fish assemblage catch-per-unit-effort (CPUE) (fish per hour) (open triangles, dotted lines- W. Tonn and A. Danylchuk, unpublished data) over time in LLB800. Points are means and vertical bars represent 1 *S.E.*.

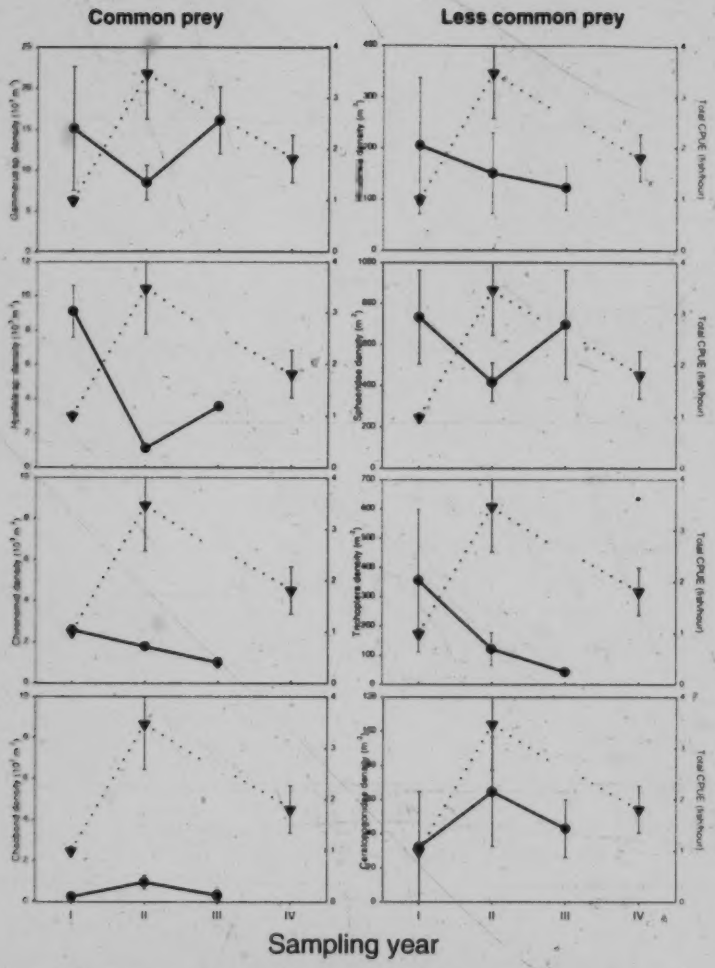

Figure 3.2. Macroinvertebrate densities (filled circles, solid lines) and total fish assemblage catch-per-unit-effort (CPUE) (fish per hour) (open triangles, dotted lines- W. Tonn and A. Danylchuk, unpublished data) over time in SPH20. Points are means and vertical bars represent 1 *S.E.*.

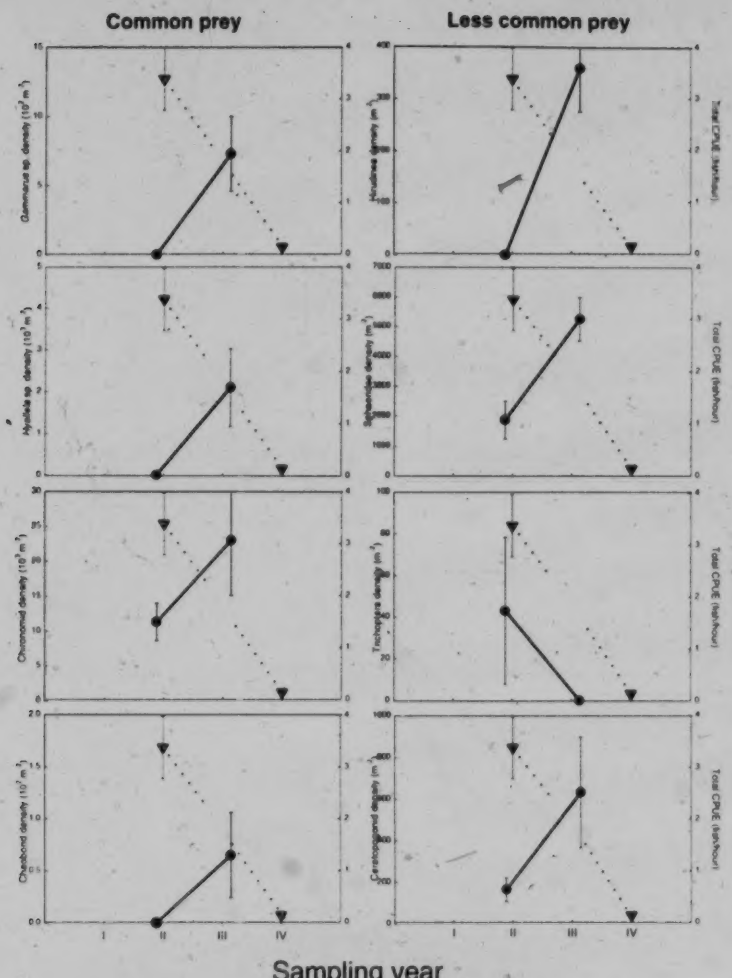

Figure 3.3. Macroinvertebrate densities (filled circles, solid lines) and total fish assemblage catch-per-unit-effort (CPUE) (fish per hour) (open triangles, dotted lines-W. Tonn and A. Danylchuk, unpublished data) over time in SPH800. Points are means and vertical lines represent 1 *S.E.*.

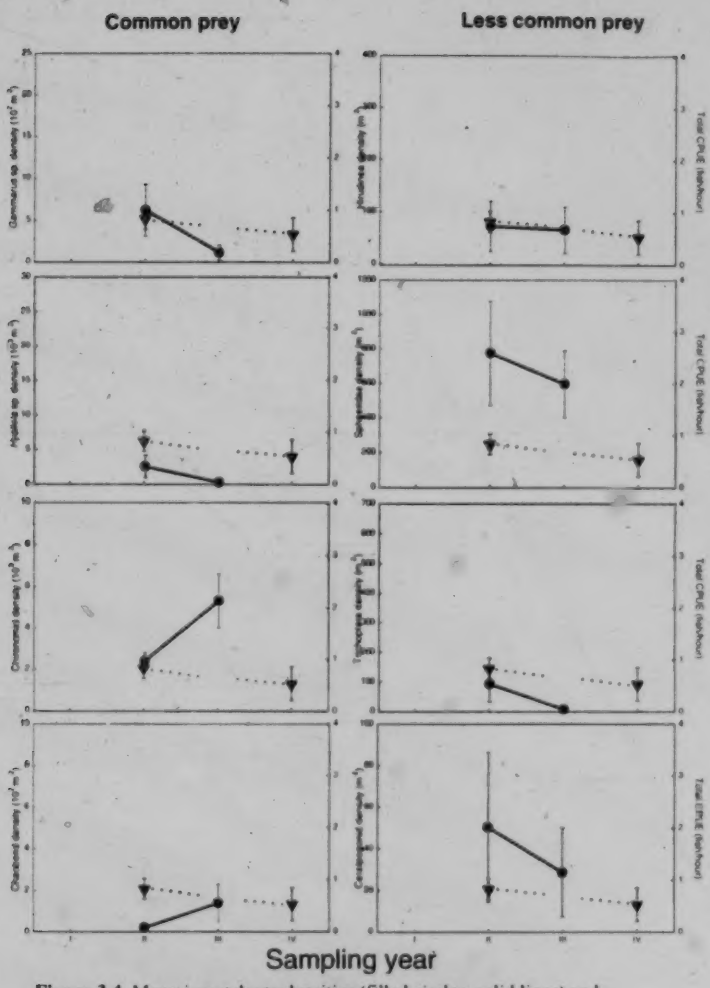

Figure 3.4. Macroinvertebrate densities (filled circles, solid lines) and total fish assemblage catch-per-unit-effort (CPUE) (fish per hour) (open triangles, dotted lines- W. Tonn and A. Danylchuk, unpublished data) over time in LLB20. Points are means and vertical lines represent 1 *S.E.*

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Chapter 4

4.1 General Discussion and Conclusions

Increased allocation of land for resource extraction in the Boreal Plain of north-central Alberta has elevated the demand for knowledge of the natural dynamics of undisturbed ecosystems. The Terrestrial and Riparian Organisms, Lakes and Streams (TROLS) project was designed to document natural ecosystem functions and determine the effects of timber harvest in aspen-dominated watersheds on terrestrial and aquatic habitats of Alberta's Boreal Plain. Bridging the pre- and post-harvest portions of the TROLS project, my study was important for developing an understanding of the structure of littoral macroinvertebrate communities as it relates to natural gradients in key environmental factors among lakes on the Boreal Plain.

Investigation of the functional relationships between littoral macroinvertebrate communities of lakes on the Boreal Plain and their chemical, physical, and biological environment revealed both similarities and differences with previously studied macroinvertebrate communities in north temperate regions. Macroinvertebrate community taxonomic and numerical composition and seasonality were similar to that observed in other lakes on the Boreal Plain (Yee, 1997), and across boreal North America (*e.g.*, Cooper, 1965; Dermott, 1988; Wen, 1992), suggesting that my results may apply to nutrient-rich boreal regions outside of the Boreal Plain. The role that different environmental factors have in structuring littoral macroinvertebrate communities is a widely debated subject, with different researchers arguing, for example, the importance of nutrients (Dermott *et al.* 1977; Clarke, Knoechel & Ryan, 1997), lake-basin characteristics (Rasmussen & Kalff, 1987; Rasmussen, 1988a), and fish (Post & Cucin, 1984; Dermott, 1988) to benthic food webs. In my study, littoral macroinvertebrate

biomass was positively associated with TP concentration in stratified lakes, implying that bottom-up energy transfers may contribute to benthic food webs in thermally stable lakes. However, in polymictic lakes, macroinvertebrate taxonomic richness was negatively related to TP concentration, and macroinvertebrate biomass was not related to TP concentration. These relationships would suggest that low dissolved oxygen availability may begin to offset the benefits of increased nutrient concentration in increasingly nutrient-rich and thermally unstable lakes. The observed positive relationship between community diversity and thermal stability supports this line of thought, in that littoral macroinvertebrate communities in stratified lakes were more diverse and were less likely to be exposed to low dissolved oxygen concentrations than those of polymictic lakes. My observations of littoral macroinvertebrate density and fish density over time (either measured or projected) indicate that benthivorous pike and perch may reduce the abundance and relative density of common prey organisms such as *Gammarus* sp. and *Hyallela* sp. in lakes on the Boreal Plain. Thus, where environmental conditions may be harsh (*i.e.*, in eutrophic to hypereutrophic, polymictic lakes) littoral macroinvertebrate community structure is likely negatively influenced by low dissolved oxygen concentration. In contrast, where less environmentally harsh conditions prevail (*i.e.*, in mesotrophic to eutrophic, stratified lakes) the bottom-up influences of nutrients are likely positive. Further, my results provide evidence that the top-down influences of predation by pike and perch are important to the development of littoral macroinvertebrate community structure in lakes on the Boreal Plain.

Investigation of temporal and spatial dissolved oxygen dynamics in the littoral zone, and the influence of primary producers (*i.e.*, algae and macrophytes) on these

dynamics would help determine how these ecological factors contribute to the structure of littoral macroinvertebrate communities in boreal lakes. In my study, *Hyallela* sp. and macrophyte biomass were negatively related. Previously reported relationships between basin slope, macrophyte bed composition, and dissolved oxygen concentration suggest that these factors are likely to influence macroinvertebrate communities, especially in systems where nutrients and food may not be limiting (Rasmussen, 1988b; Duarte & Kalff, 1986; Davies & Gates, 1991).

My study showed that littoral macroinvertebrate communities are related to TP concentration, thermal stability, and predatory fish density in lakes on the Boreal Plain. These relationships, if extrapolated, may imply that anthropogenic disturbances that either enhance nutrient concentration, lessen thermal stability, or alter fish densities, may ultimately influence benthic macroinvertebrate assemblages in lakes on the Boreal Plain. Among lakes on the Boreal Plain, the littoral macroinvertebrate communities of currently mesotrophic to eutrophic and weakly thermally stratified lakes would be expected to be most sensitive to such disturbances. Where maintenance of littoral macroinvertebrate community structure is a concern, land-use practices designed to moderate changes in nutrient concentration and thermal structure of the water column should be implemented.

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Appendix A:

Whole-lake average littoral macroinvertebrate densities in the seven study lakes in 1996-1997.

Table A1. Mean densities (+/- *S.E.*) of littoral macroinvertebrate taxa in LLB20 shortly after ice-out (Spring-96), in mid-summer 1996, and mid-summer 1997.

	Spring-96		Mid-summer-96		Mid-summer-97	
Taxa	Mean	*S.E.*	Mean	*S.E.*	Mean	*S.E.*
Chironomidae (larvae)	4834.4	1025.3	10846.8	3338.1	10336.8	3392.4
Chironomidae (pupae)	14.4	14.4	100.6	45.4	100.6	34.6
Chaoboridae (larvae)	7.2	7.2	21.6	14.7	143.7	89.5
Chaoboridae (pupae)	--	--	--	--	--	--
Ceratopogonidae	158.0	90.2	64.7	36.5	79.0	34.2
Hyallelidae	2571.6	440.6	3483.9	2415.1	301.7	284.6
Gammaridae	208.3	46.5	617.8	313.4	100.6	92.2
Hirudinea	43.1	15.7	71.8	48.1	64.7	44.2
Platyhelminthes	35.9	23.4	1012.9	472.1	21.6	21.6
Oligochaeta	969.8	159.7	7521	5693.8	2370.5	917.2
Nematoda	3189.4	1591.4	2327.4	868.3	12039.3	2984.2
Sphaeridae	603.4	170.6	991.3	361.7	783	252.9
Acari	301.7	137.2	258.6	137.2	122.1	58.3
Phryganeidae	--	--	57.5	41.1	7.2	7.2
Trichoptera (Immature)	--	--	21.6	14.7	--	--
Leptoceridae	--	--	14.4	14.4	--	--
Limnephilidae	--	--	14.4	14.4	--	--
Molannidae	--	--	--	--	--	--
Trichoptera (pupae)	--	--	--	--	--	--
Hydroptilidae	--	--	--	--	--	--
Polycentropodidae	7.2	7.2	--	--	--	--
Caenidae	--	--	100.6	53	--	--
Chloroperlidae	--	--	--	--	--	--
Coenagriondae	--	--	--	--	--	--
Corduliidae	--	--	--	--	--	--
Corixidae	--	--	--	--	--	--
Notonectidae	--	--	--	--	--	--
Coleoptera-larva	--	--	7.2	7.2	--	--
Chrysomelidae (pupae)	--	--	--	--	--	--
Zygoptera	--	--	--	--	--	--
Lymnaeadae	14.4	14.4	21.6	14.7	28.7	28.7
Planorbidae	--	--	28.7	14.4	--	--
Physidae	--	--	--	--	--	--
Unionidae	--	--	--	--	--	--
Conchostraca	--	--	--	--	--	--
Total density	12958.7	1804.0	27591.2	6219.2	26499.3	6885.9
Total # of taxa	14		20		14	

Table A2. Mean densities (+/- *S.E.*) of littoral macroinvertebrate taxa in LLB800 shortly after ice-out (Spring-96), in mid-summer 1996, and mid-summer 1997.

	Spring-96		Mid-summer-96		Mid-summer-97	
Taxa	Mean	*S.E.*	Mean	*S.E.*	Mean	*S.E.*
Chironomidae (larvae)	8239.3	3764.4	36074.7	12274.4	6852.9	3563.4
Chironomidae (pupae)	172.4	164.0	194	46.9	136.5	136.5
Chaoboridae (larvae)	7.2	7.2	7.2	7.2	725.5	190
Chaoboridae (pupae)	--	--	--	--	--	--
Ceratopogonidae	2205.3	849.6	1379.2	435.8	251.4	95.4
Hyallelidae	4360.3	1195.9	25996.5	5365.2	3376.2	2204.8
Gammaridae	265.8	105.3	1716.8	530	596.2	206.6
Hirudinea	14.4	9.1	136.5	40.8	308.9	66.2
Platyhelminthes	--	--	--	--	--	--
Oligochaeta	423.8	159.5	1249.9	332.8	912.3	386.9
Nematoda	122.1	62.4	639.3	153.6	2255.6	938.1
Sphaeridae	2471.1	832.9	2370.5	515.5	3009.8	838.7
Acari	79.0	34.2	107.8	36.5	150.9	34.8
Phryganeidae	35.9	20.6	--	--	--	--
Trichoptera (Immature)	47.4	12.1	64.7	31	--	--
Leptoceridae	150.9	109.5	7.2	7.2	--	--
Limnephilidae	--	--	--	--	--	--
Molannidae	21.6	14.7	14.4	9.1	14.4	9.1
Trichoptera (pupae)	--	--	7.2	7.2	--	--
Hydroptilidae	--	--	--	--	--	--
Polycentropodidae	--	--	--	--	--	--
Caenidae	57.5	26.5	7.2	7.2	--	--
Chloroperlidae	--	--	--	--	--	--
Coenagriondae	--	--	--	--	--	--
Corduliidae	--	--	--	--	--	--
Corixidae	--	--	21.6	14.7	--	--
Notonectidae	--	--	--	--	28.7	14.4
Coleoptera-larva	--	--	--	--	--	--
Chrysomelidae (pupae)	--	--	--	--	--	--
Zygoptera	--	--	--	--	--	--
Lymnaeadae	--	--	14.4	14.4	--	--
Planorbidae	--	--	--	--	--	--
Physidae	--	--	--	--	7.2	7.2
Unionidae	--	--	--	--	--	--
Conchostraca	--	--	--	--	--	--
Total density	18676.7	4504.7	70016	16684.7	18626.4	7293.2
Total # of taxa	16		19		14	

Table A3. Mean densities (+/- *S.E.*) of littoral macroinvertebrate taxa in SCL20 shortly after ice-out (Spring-96), in mid-summer 1996, and mid-summer 1997.

	Spring-96		Mid-summer-96		Mid-summer-97	
Taxa	Mean	*S.E.*	Mean	*S.E.*	Mean	*S.E.*
Chironomidae (larvae)	1350.5	347.0	14460.1	2553.4	2083.2	856.2
Chironomidae (pupae)	150.9	113.4	423.8	120.1	--	--
Chaoboridae (larvae)	--	--	--	--	--	--
Chaoboridae (pupae)	--	--	--	--	--	--
Ceratopogonidae	21.6	21.6	7.2	7.2	7.2	7.2
Hyallelidae	474.1	148.9	4992.4	1305.6	545.9	224.7
Gammaridae	--	--	1314.6	258.6	143.7	56.4
Hirudinea	--	--	21.6	9.6	21.6	14.7
Platyhelminthes	--	--	--	--	--	--
Oligochaeta	352.0	95.4	3879.0	1220.1	122.1	42.3
Nematoda	35.9	23.4	1573.2	811.7	337.6	220.5
Sphaeridae	14.4	9.1	1214	409	1652.2	591.6
Acari	64.7	18.5	423.8	373.7	--	--
Phryganeidae	--	--	--	--	--	--
Trichoptera (Immature)	--	--	50.3	28.2	--	--
Leptoceridae	--	--	--	--	--	--
Limnephilidae	--	--	14.4	9.1	--	--
Molannidae	28.7	14.4	43.1	22.3	165.2	60.4
Trichoptera (pupae)	--	--	--	--	--	--
Hydroptilidae	--	--	--	--	--	--
Polycentropodidae	--	--	--	--	--	--
Caenidae	28.7	28.7	--	--	--	--
Chloroperlidae	--	--	--	--	--	--
Coenagriondae	--	--	--	--	--	--
Corduliidae	--	--	--	--	--	--
Corixidae	--	--	21.6	14.7	--	--
Notonectidae	--	--	--	--	--	--
Coleoptera-larva	--	--	--	--	--	--
Chrysomelidae (pupae)	--	--	--	--	--	--
Zygoptera	--	--	--	--	--	--
Lymnaeadae	--	--	--	--	--	--
Planorbidae	--	--	--	--	--	--
Physidae	--	--	--	--	--	--
Unionidae	--	--	--	--	--	--
Conchostraca	--	--	--	--	--	--
Total density	2521.4	335.4	28438.8	4283.5	5078.6	667.6
Total # of taxa	10		14		9	

Table A4. Mean densities (+/- *S.E.*) of littoral macroinvertebrate taxa in SCL800 shortly after ice-out (Spring-96), in mid-summer 1996, and mid-summer 1997.

	Spring-96		Mid-summer-96		Mid-summer-97	
Taxa	Mean	*S.E.*	Mean	*S.E.*	Mean	*S.E.*
Chironomidae (larvae)	4662.0	869.0	4791.3	1178.8	5674.8	1062.9
Chironomidae (pupae)	--	--	143.7	51.8	57.5	21.3
Chaoboridae (larvae)	43.1	19.3	14.4	14.4	158	44.1
Chaoboridae (pupae)	--	--	--	--	--	--
Ceratopogonidae	79.0	70.8	43.1	0.0	79	46.5
Hyallelidae	143.7	71.8	1242.7	683.4	14.4	9.1
Gammaridae	7.2	7.2	431	405.8	--	--
Hirudinea	71.8	14.4	79	30.3	43.1	15.7
Platyhelminthes	--	--	--	--	--	--
Oligochaeta	43.1	19.3	14.4	14.4	57.5	21.3
Nematoda	28.7	14.4	43.1	22.3	7.2	7.2
Sphaeridae	704.0	227.7	237.1	139.4	402.3	153.7
Acari	747.1	273.5	150.9	46.9	43.1	11.1
Phryganeidae	35.9	28.2	7.2	7.2	--	--
Trichoptera (Immature)	--	--	--	--	--	--
Leptoceridae	--	--	--	--	--	--
Limnephilidae	--	--	--	--	--	--
Molannidae	14.4	14.4	--	--	--	--
Trichoptera (pupae)	--	--	--	--	--	--
Hydroptilidae	7.2	7.2	7.2	7.2	--	--
Polycentropodidae	--	--	--	--	--	--
Caenidae	114.9	42.6	14.4	9.1	7.2	7.2
Chloroperlidae	--	--	--	--	--	--
Coenagriondae	--	--	--	--	7.2	7.2
Corduliidae	7.2	7.2	--	--	21.6	14.7
Corixidae	--	--	--	--	--	--
Notonectidae	--	--	7.2	7.2	--	--
Coleoptera-larva	--	--	--	--	--	--
Chrysomelidae (pupae)	--	--	--	--	--	--
Zygoptera	--	--	--	--	--	--
Lymnaeadae	--	--	--	--	--	--
Planorbidae	57.5	18.2	574.7	152.5	--	--
Physidae	--	--	--	--	--	--
Unionidae	--	--	--	--	--	--
Conchostraca	--	--	--	--	7.2	7.2
Total density	6788.3	1332.5	7801.1	991.5	6587.1	1090
Total # of taxa	16		16		14	

Table A5. Mean densities (+/- *S.E.*) of littoral macroinvertebrate taxa in SPH20 shortly after ice-out (Spring-96), in mid-summer 1996, and mid-summer 1997.

	Spring-96		Mid-summer-96		Mid-summer-97	
Taxa	Mean	*S.E.*	Mean	*S.E.*	Mean	*S.E.*
Chironomidae (larvae)	4367.5	1975.7	5567.1	1542.7	4417.8	1894.1
Chironomidae (pupae)	--	--	28.7	14.4	50.3	42.3
Chaoboridae (larvae)	14.4	9.1	136.5	34.2	28.7	21.3
Chaoboridae (pupae)	--	--	--	--	--	--
Ceratopogonidae	35.9	20.6	114.9	50.6	50.3	20.6
Hyallelidae	574.7	171.2	2356.1	1086.8	4604.5	912.9
Gammaridae	150.9	67.5	847.6	198.4	1609.1	377.6
Hirudinea	14.4	14.4	150.9	70.2	229.9	106
Platyhelminthes	7.2	7.2	64.7	56.5	100.6	50.6
Oligochaeta	143.7	41.1	359.2	98.1	531.6	183.5
Nematoda	100.6	53.0	79	37.6	682.4	349.2
Sphaeridae	380.7	202.6	876.4	188.1	1810.2	847.7
Acari	7.2	7.2	122.1	43.7	100.6	14.4
Phryganeidae	--	--	28.7	18.2	--	--
Trichoptera (Immature)	--	--	646.5	443.4	14.4	9.1
Leptoceridae	--	--	--	--	--	--
Limnephilidae	--	--	--	--	7.2	7.2
Molannidae	--	--	57.5	49.4	--	--
Trichoptera (pupae)	--	--	--	--	7.2	7.2
Hydroptilidae	--	--	--	--	--	--
Polycentropodidae	114.9	71.8	35.9	35.9	21.6	9.6
Caenidae	7.2	7.2	64.7	34.8	7.2	7.2
Chloroperlidae	--	--	12.9	12.9	--	--
Coenagriondae	7.2	7.2	28.7	18.2	--	--
Corduliidae	--	--	--	--	--	--
Corixidae	--	--	--	--	--	--
Notonectidae	--	--	--	--	--	--
Coleoptera-larva	7.2	7.2	--	--	--	--
Chrysomelidae (pupae)	--	--	7.2	7.2	--	--
Zygoptera	--	--	--	--	--	--
Lymnaeadae	7.2	7.2	35.9	28.2	8.6	7.9
Planorbidae	--	--	7.2	7.2	--	--
Physidae	7.2	7.2	--	--	--	--
Unionidae	--	--	--	--	--	--
Conchostraca	--	--	--	--	--	--
Total density	5969.4	2231.2	11644.2	1933	14287.7	2447.2
Total # of taxa	17		22		18	

Table A6. Mean densities (+/- *S.E.*) of littoral macroinvertebrate taxa in SPH800 shortly after ice-out (Spring-96), in mid-summer 1996, and mid-summer 1997.

	Spring-96		Mid-summer-96		Mid-summer-97	
Taxa	Mean	*S.E.*	Mean	*S.E.*	Mean	*S.E.*
Chironomidae (larvae)	11004.9	972.4	16141.0	3910.2	43035.4	11983.3
Chironomidae (pupae)	352.0	91.4	201.1	65.5	79	63.4
Chaoboridae (larvae)	352.0	114.3	7.2	7.2	79	55
Chaoboridae (pupae)	--	--	--	--	--	--
Ceratopogonidae	301.7	77.9	165.2	57.2	632.1	266.4
Hyallelidae	129.3	75.5	43.1	22.3	2126.3	942.2
Gammaridae	28.7	28.7	--	--	732.7	274.7
Hirudinea	14.4	9.1	--	--	366.4	88.2
Platyhelminthes	--	--	--	--	--	--
Oligochaeta	660.9	274.8	179.6	67.2	459.7	160
Nematoda	86.2	45.9	14.4	9.1	165.2	148.3
Sphaeridae	5344.4	2048.2	2636.3	928.3	7499.4	1209.2
Acari	423.8	127.6	445.4	243	229.9	120.2
Phryganeidae	--	--	7.2	7.2	--	--
Trichoptera (Immature)	--	--	43.1	29.4	--	--
Leptoceridae	--	--	--	--	--	--
Limnephilidae	--	--	--	--	--	--
Molannidae	--	--	--	--	--	--
Trichoptera (pupae)	7.2	7.2	--	--	--	--
Hydroptilidae	7.2	7.2	--	--	--	--
Polycentropodidae	50.3	25.9	--	--	--	--
Caenidae	273.0	45.4	14.4	9.1	7.2	7.2
Chloroperlidae	--	--	--	--	--	--
Coenagriondae	43.1	29.4	7.2	7.2	--	--
Corduliidae	57.5	41.1	14.4	9.1	7.2	7.2
Corixidae	--	--	7.2	7.2	--	--
Notonectidae	--	--	--	--	14.4	9.1
Coleoptera-larva	--	--	--	--	--	--
Chrysomelidae (pupae)	--	--	--	--	--	--
Zygoptera	--	--	7.2	7.2	--	--
Lymnaeadae	--	--	--	--	--	--
Planorbidae	165.2	35.9	186.8	75.2	474.1	170.6
Physidae	--	--	7.2	7.2	--	--
Unionidae	--	--	--	--	35.9	20.6
Conchostraca	--	--	--	--	--	--
Total density	19301.6	1968.8	20127.7	4902.5	55958.2	13909.7
Total # of taxa	18		18		16	

Table A7. Mean densities (+/- *S.E.*) of littoral macroinvertebrate taxa in SPH100 shortly after ice-out (Spring-96), in mid-summer 1996, and mid-summer 1997.

	Spring-1996		Mid-summer-96		Mid-summer-97	
Taxa	Mean	*S.E.*	Mean	*S.E.*	Mean	*S.E.*
Chironomidae (larvae)	--	--	6134.6	1527.6	1091.9	267.3
Chironomidae (pupae)	--	--	50.3	20.6	--	--
Chaoboridae (larvae)	--	--	596.2	270	4389	523.9
Chaoboridae (pupae)	--	--	--	--	--	--
Ceratopogonidae	--	--	57.5	21.3	21.6	14.7
Hyallelidae	--	--	--	--	--	--
Gammaridae	--	--	7.2	7.2	--	--
Hirudinea	--	--	71.8	32.8	28.7	21.3
Platyhelminthes	--	--	--	--	--	--
Oligochaeta	--	--	64.7	32.9	28.7	9.1
Nematoda	--	--	43.1	19.3	28.7	14.4
Sphaeridae	--	--	43.1	27.3	50.3	23.4
Acari	--	--	93.4	30.3	--	--
Phryganeidae	--	--	--	--	--	--
Trichoptera (Immature)	--	--	--	--	--	--
Leptoceridae	--	--	--	--	--	--
Limnephilidae	--	--	--	--	--	--
Molannidae	--	--	--	--	--	--
Trichoptera (pupae)	--	--	--	--	--	--
Hydroptilidae	--	--	--	--	--	--
Polycentropodidae	--	--	--	--	--	--
Caenidae	--	--	7.2	7.2	--	--
Chloroperlidae	--	--	--	--	--	--
Coenagriondae	--	--	--	--	--	--
Corduliidae	--	--	--	--	--	--
Corixidae	--	--	--	--	--	--
Notonectidae	--	--	--	--	--	--
Coleoptera-larva	--	--	--	--	--	--
Chrysomelidae (pupae)	--	--	--	--	--	--
Zygoptera	--	--	--	--	--	--
Lymnaeadae	--	--	7.2	7.2	--	--
Planorbidae	--	--	--	--	--	--
Physidae	--	--	--	--	--	--
Unionidae	--	--	--	--	--	--
Conchostraca	--	--	--	--	--	--
Mean density	--	--	7176.2	1576.9	5782.6	603.8
Total # of taxa	--	--	12		10	

Appendix B:

Littoral macroinvertebrate densities and biomasses for 1996 and 1997.

Table B1. LLB20 benthic macroinvertebrate density (#individuals/sample) and dry weight biomass (g/sample) data for spring 1996, late summer 1996, and late summer 1997 sampling trips.

LLB20 May 9th, 1996				LLB20 July 27th, 1996				LLB20 August 16th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)		taxa	#/grab	weight (g)
sample L1 @ 2m				sample L1 @ 2.7m				sample L1 @ 2.4m			
4mm	Chironomidae (L)	31	0.0061	4mm	*Gammarus*	12	arch	1mm	Chironomidae (L)	219	arch
	Gammarus	3	0.0138		Oligochaeta	9	arch		*Hyallela*	1	arch
	Ceratopogonidae	1	--		Nematoda	3	arch		Oligochaeta	32	arch
	Oligochaeta	1	0.0002		Platyhelminthes	2	arch		Nematoda	43	arch
1mm	*Hyallela*	20	0.0099	1mm	Chironomidae (L)	35	arch		Sphaeridae	2	arch
	Chironomidae (L)	73	0.0088		Oligochaeta	12	arch		*Chaoborus*	1	arch
	Oligochaeta	7	0.0003		Sphaeridae	8	arch		Chironomidae (P)	1	arch
	Nematoda	13	0.001		Nematoda	3	arch	250u	Chironomidae (L)	68	arch
	Ostracoda	2	--		Lymnaeadae	1	arch		Nematoda	294	arch
250u	Chironomidae (L)	11	0.0008		Platyhelminthes	4	arch		Oligochaeta	36	arch
	Oligochaeta	4	--	250u	Chironomidae (L)	148	arch		Ostracoda	378	arch
	Ostracoda	23	--		Oligochaeta	19	arch	total	8	1075	
	Nematoda	89	0.0009		Ostracoda	496	arch				
	Acari	1	--		Nematoda	7	arch				
total	8	279			*Hyallela*	1	arch	sample L3 @ 1.6m			
					Acari	1	arch	1mm	Chironomidae (L)	101	0.0093
					Planorbidae	1	arch		Oligochaeta	12	0.0013
sample L3 @ 3m				total	11	762			Nematoda	14	--
4mm	*Gammarus*	3	arch						*Chaoborus*	13	0.0009
1mm	*Hyallela*	66	arch						Sphaeridae	3	0.0012
	Sphaeridae	13	arch	sample L2 @ 2.7m					Acari	1	0.0003
	Oligochaeta	6	arch	1mm	Chironomidae (P)	2	0.0002	250u	Chironomidae (L)	32	0.0017
	Lymnaeadae	2	arch		Chironomidae (L)	73	0.006		Oligochaeta	14	0.0017
	Chironomidae (L)	13	arch		Oligochaeta	31	0.0026		Nematoda	382	0.0033
	Acari	7	arch		Nematoda	3	--		Ostracoda	175	--

Table B1: Continued

LLB20 May 9th, 1996				LLB20 July 27th, 1996				LLB20 August 16th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight		taxa	#/grab	weight
	Platyhelminthes	2	arch		*Hyallela*	9	0.0013	total	7	747	
	Nematoda	2	arch		Sphaeridae	4	0.0012				
250u	Chironomidae (L)	35	arch		Platyhelminthes	21	0.005				
	Ceratopogonidae	2	arch		Acari	3	0.0002	sample	L6 @ 2.5m		
	Oligochaeta	20	arch		*Chaoborus*	1	--	4mm	Chironomidae (L)	3	0.0044
	Ostracoda	13	arch		Lymnaeadae	2	0.0031		Sphaeridae	1	0.009
	Acari	14	arch	250u	Chironomidae (L)	165	0.0027	1mm	Chironomidae (P)	5	0.0059
	Nematoda	5	arch		Nematoda	20	--		Chironomidae (L)	12	0.0043
	Sphaeridae	13	arch		Oligochaeta	42	0.0016		Oligochaeta	8	0.0005
	Platyhelminthes	1	arch		Platyhelminthes	4	0.0004		Nematoda	14	1E-04
total	11	217	arch		Acari	5	0.0002		Acari	9	0.0044
					Ostracoda	610	--		Sphaeridae	11	0.0057
					Sphaeridae	2	--		Ceratopogonidae	1	--
sample	L4 @ 2m				Chironomidae (P)	1	--		*Hyallela*	1	--
4mm	*Gammarus*	2	0.0103		Planorbidae	1	--	250u	Chironomidae (L)	13	--
	Hirudinea	2	0.0446		Trich:immature	1	--		Oligochaeta	12	0.0003
	Ceratopogonidae	1	0.0002	total	13	1000			Nematoda	18	0.0004
1mm	Oligochaeta	8	0.0011						*Chaoborus*	1	--
	Hyallela	63	0.0243						Ostracoda	76	--
	Chironomidae (L)	28	0.0053	sample	L3 @ 2.8m				Ceratopogonidae	2	0.0003
	Sphaeridae	2	0.0001	1mm	Chironomidae (P)	7	0.0006	total	10	187	
	Nematoda	2	--		Chironomidae (L)	81	0.0028				
	Chaoborus	1	--		*Chaoborus*	2	--				
	Platyhelminthes	1	1E-04		Acari	1	--	sample	C2 @ 1.9m		
250u	Chironomidae (L)	91	0.002		*Hyallela*	4	1E-04	1mm	Chironomidae (P)	4	0.0029
	Oligochaeta	10	0.0006		Oligochaeta	3	--		Chironomidae (L)	142	0.0174
	Nematoda	15	0.0006		Nematoda	19	0.0003		Oligochaeta	9	0.001

Table B1: Continued

LLB20 May 9th, 1996				LLB20 July 27th, 1996				LLB20 August 16th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight		taxa	#/grab	weight
	Ostracoda	59	0		Platyhelminthes	3	0.0003		Nematoda	135	0.0016
	Platyhelminthes	1	--	250u	Chironomidae (L)	542	0.0029		Sphaeridae	14	0.0181
	Ceratopogonidae	2	--		Nematoda	57	0.0018		Acari	1	--
	Sphaeridae	4	--		Oligochaeta	18	0.0017		Hirudinea-small	3	0.0054
	Acari	5	--		Ostracoda	750	0		*Gammarus*	1	0.0006
total	12	297			Acari	2	1E-04	250u	Chironomidae (L)	58	0.0026
sample C1 @ 2m					Ephemeroptera	8	0.0003		Oligochaeta	8	0.0014
4mm	*Gammarus*	5	0.0269	final	10	1497			Nematoda	68	0.0012
	Hirudinea	1	0.0076						Sphaeridae	12	0.0011
1mm	Chironomidae (L)	36	0.0139						Ceratopogonidae	1	0.006
	Hyallela	57	0.0173	sample C1 @ 2.3m					Ostracoda	165	--
	Oligochaeta	3	0.0007	4mm	*Gammarus*	2	0.0086	total	10	621	
	Nematoda	31	--		Sphaeridae	1	0.0147				
	Ceratopogonidae	8	0.0002		Oligochaeta	7	0.0031				
	Sphaeridae	12	0.0059		Phryganeidae	1	0.0005	sample C3 @ 2.2m			
	Hirudinea	1	--	1mm	Chironomidae (L)	19	0.0012	4mm	Hirudinea	1	0.006
	Gammarus	1	0.0019		*Gammarus*	46	0.0216	1mm	Chironomidae (P)	3	0.0006
250u	Chironomidae (L)	22	--		*Hyallela*	235	0.0227		Chironomidae (L)	63	0.0129
	Ostracoda	201	--		Chironomidae (P)	2	0.0003		Oligochaeta	3	--
	Nematoda	213	--		Oligochaeta	24	0.0053		Nematoda	14	--
	Ceratopogonidae	6	0.0003		Platyhelminthes	6	0.0016		*Gammarus*	13	0.0103
	Oligochaeta	25	0.0008		Sphaeridae	18	0.0242		*Hyallela*	40	0.0083
	Sphaeridae	1	--		Nematoda	4	--		Hirudinea	5	0.0146
	Acari	1	--		Acari	3	1E-04		Sphaeridae	21	0.0135
total	10	624			Ceratopogonidae	2	0.0005		Platyhelminthes	3	--
					Leptoceridae	1	--		Lymnaeadae	4	0.0055
					Hirudinea	1	--		Acari	2	--

Table B1: Continued

LLB20 May 9th, 1996				LLB20 July 27th, 1996				LLB20 August 16th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight		taxa	#/grab	weight
sample C2 @ 2m				250u	Chironomidae (L)	69	0.001		Phryganeidae	1	0.0012
4mm	*Gammarus*	4	0.0222		*Hyallela*	119	0.0036	250u	Chironomidae (L)	136	0.0013
1mm	Chironomidae (L)	38	0.0053		Acari	18	0.0013		Oligochaeta	42	0.0006
	Hyallela	54	0.0179		Ostracoda	193	0		Nematoda	184	0.0008
	Gammarus	2	0.007		Sphaeridae	17	0.0013		Sphaeridae	13	0.0012
	Oligochaeta	6	0.0029		Nematoda	17	0		Ceratopogonidae	2	0.0006
	Acari	1	1E-04		Ephemeroptera	3	--		Ostracoda	87	--
	Sphaeridae	8	0.0037		Oligochaeta	6	--	total	14	637	
	Hirudinea	1	0.0004		Leptoceridae	1	--				
250u	Chironomidae (L)	84	0.0023		Ceratopogonidae	1	1E-04	sample C4 @ 3m			
	Sphaeridae	10	0.0007	total	15	816		4mm	Chironomidae (L)	7	0.0091
	Ostracoda	67	--					1mm	Chironomidae (P)	1	0.0003
	Acari	10	--						Chironomidae (L)	183	0.0078
	Oligochaeta	9	--	sample C2@2.5m					Oligochaeta	22	0.0058
	Nematoda	18	1E-04	1mm	Chironomidae (L)	51	0.001		Nematoda	105	0.0007
	Ceratopogonidae	1	--		*Gammarus*	17	0.0076		Ceratopogonidae	3	--
total	10	313			*Hyallela*	76	0.0107		Sphaeridae	31	0.021
					Platyhelminthes	73	0.0204		Acari	4	0.0009
					Sphaeridae	41	0.0246		*Chaoborus*	5	--
sample C3 @ 2m					Coleoptera:Gyrinidae	1	--	250u	Chironomidae (L)	402	0.0051
4mm	*Gammarus*	8	0.0097		Nematoda	12	--		Oligochaeta	132	0.0046
	Hirudinea	1	0.0694		Oligochaeta	24	0.001		Nematoda	405	0.0055
1mm	Chironomidae (L)	94	0.0166		Hirudinea	2	--		Ceratopogonidae	2	0.0002
	Hyallela	98	0.0396		Snail	1	0.0019		Sphaeridae	1	--
	Sphaeridae	19	0.0145		Trich:Phryganeidae	1	0.0003		Ostracoda	95	--
	Nematoda	6	--		Acari	1	--	total	9	1398	
	Oligochaeta	12	0.0006	250u	Chironomidae (L)	173	0.0035				

Table B1: Continued

LLB20 May 9th, 1996				LLB20 July 27th, 1996				LLB20 August 16th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa		weight #/grab		taxa		weight #/grab
	Gammarus	1	0.0032		*Hyallela*	6	--				
	Ostracoda	1	--		Nematoda	36	--				
	Trich:polycentropus	1	0.0017		Oligochaeta	18	1E-04				
	Chironomidae (P)	1	0.0002		Sphaeridae	6	--				
	Acari	1	0.0002		Platyhelminthes	1	--				
250u	Chironomidae (L)	117	0.0022		Ostracoda	330	0				
	Ostracoda	55	--		Ephemeroptera	1	--				
	Nematoda	50	1E-04		Ceratopogonidae	1	--				
	Oligochaeta	24	0.0006	total	15	872					
	Sphaeridae	2	--								
	Ceratopogonidae	1	--	sample C4 @ 2.5m							
	Acari	2	1E-04	4mm	Phryganeidae	1	0.0009				
	Chironomidae (P)	1	--		Oligochaeta	2	0.0006				
total	12	495		1mm	Chironomidae (P)	1	--				
					Chironomidae (L)	64	0.0028				
					Oligochaeta	421	0.0613				
					Nematoda	84	0.0007				
					Sphaeridae	36	0.0145				
					Platyhelminthes	21	0.0027				
					Gammarus	9	0.004				
					Hyallela	35	0.0052				
					Ostracoda	1	--				
					Hirudinea	7	0.0038				
					Ceratopogonidae	5	--				
					Phryganeidae	6	0.004				

Table B1: Continued

LLB20 May 9th, 1996				LLB20 July 27th, 1996				LLB20 August 16th, 1997	
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight	taxa	#/grab weight
					Limnephilidae	2	--		
				250u	Chironomidae (P)	1	--		
					Chironomidae (L)	90	0.0012		
					Oligochaeta	411	0.0143		
					Nematoda	59	--		
					Platyhelminthes	6	--		
					Acari	2	--		
					Ostracoda	108	--		
					Sphaeridae	5	--		
					Ephemeroptera	2	--		
					Trichoptera	2	--		
					Planorbidae	2	--		
				total	17	1383			

Table B2. LLB800 benthic macroinvertebrate density (#individuals/sample) and dry weight biomass (g/sample) data for spring 1996, late summer 1996, and late summer 1997 sampling trips.

LLB800 May 12th, 1996				LLB800 July 28th, 1996				LLB800 August 15th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
sample L1 @ 2m				sample L2 @ 2m				sample L1 @ 2.4m			
4mm	Chironomidae (L)	1	1E-04	4mm	*Gammarus*	1	0.0043	4mm	Physidae	1	0.0193
	Gammarus	3	0.0146		Oligochaeta	1	0.0004		Oligochaeta	1	--
	Oligochaeta	5	0.0075		Molannidae	1	0.0074	1mm	Chironomidae (L)	9	0.0028
	Molannidae	1	0.0002	1mm	Chironomidae (P)	4	1E-04		*Gammarus*	4	0.0008
1mm	Chironomidae (L)	28	0.0017		Chironomidae (L)	241	0.0086		*Hyallela*	32	0.0045
	Hyallela	123	0.0641		*Hyallela*	516	0.0455		*Chaoborus*	5	0.0008
	Sphaeridae	128	0.0209		Oligochaeta	11	0.005		Sphaeridae	9	0.0009
	Oligochaeta	3	0.0026		*Gammarus*	34	0.0217		Acari	1	0.0003
	Ceratopogonidae	18	0.0013		Sphaeridae	30	0.0031		Oligochaeta	6	0.0007
	Chaoborus	1	--		Ceratopogonidae	6	0.0014		Nematoda	1	--
	Acari	2	--		Trichoptera	1	--		Hirudinea	2	0.0018
	Nematoda	1	--		*Chaoborus*	1	0.0005		Molannidae	1	--
	Leptoceridae	1	--		Nematoda	1	--		Ceratopogonidae	1	--
	Hirudinea	1	0.0024		Hirudinea	4	0.0046	250u	Chironomidae (L)	79	0.0005
250u	Chironomidae (L)	27	0.0007		Ostracoda	14	--		Oligochaeta	24	0.0008
	Acari	3	--		Physidae	1	0.0042		Sphaeridae	16	0.0005
	Sphaeridae	12	--	250u	Chironomidae (L)	1707	0.0071		Nematoda	22	--
	Ostracoda	97	--		*Hyallela*	136	0.0029		*Chaoborus*	1	--
	Ceratopogonidae	2	--		Sphaeridae	63	0.0007		Acari	1	--
	Oligochaeta	2	--		Acari	1	--		Ostracoda	13	--
total	13	459			Oligochaeta	30	--	total	13	229	
					Ceratopogonidae	8	0.0002				
					Nematoda	11	--				

Table B2: continued

LLB800 May 12th, 1996				LLB800 July 28th, 1996				LLB800 August 15th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
sample L2 @ 2m					Trichoptera	1	--	sample L4 @ 2.5m			
4mm	Chironomidae (L)	1	--		Ostracoda	329	--	4mm	Hirudinea	3	0.0604
	Oligochaeta	2	0.0029	total	15	3153			Molannidae	1	0.0022
1mm	Chironomidae (L)	41	0.0027						Oligochaeta	2	0.0034
	Hyallela	79	0.047					1mm	Chironomidae (P)	15	0.0022
	Sphaeridae	76	0.0111	sample L3@1.9m					Chironomidae (L)	116	0.0078
	Ceratopogonidae	49	0.003	4mm	Leptoceridae	1	0.0209		*Hyallela*	324	0.0442
	Gammarus	4	0.0145	1mm	Chironomidae (P)	6	0.0009		*Gammarus*	18	0.0172
	Oligochaeta	6	0.0011		Chironomidae (L)	163	0.0126		*Chaoborus*	8	0.0014
	Leptoceridae	1	--		*Hyallela*	508	0.0395		Sphaeridae	45	0.0033
	Caenidae	3	--		*Gammarus*	40	0.0147		Nematoda	25	--
250u	Chironomidae (L)	16	0.0005		Oligochaeta	25	0.0211		Ceratopogonidae	10	0.0017
	Sphaeridae	2	--		Nematoda	8	0.0003		Hirudinea	8	0.0135
	Ceratopogonidae	10	1E-04		Hirudinea	3	0.0056		Oligochaeta	11	0.0055
	Nematoda	2	--		Ceratopogonidae	43	0.0053		Ostracoda	7	--
	Ostracoda	16	--		Sphaeridae	23	0.0014		Notonectidae	1	0.003
total	10	308			Acari	1	--	250u	Chironomidae (P)	4	--
					Trichoptera	2	--		Chironomidae (L)	453	0.0051
					Ostracoda	2	--		Nematoda	121	--
sample L5 @ 2m				250u	Chironomidae (L)	160	0.0023		Sphaeridae	49	0.0015
4mm	*Gammarus*	11	0.0405		*Hyallela*	241	0.0057		Ceratopogonidae	1	--
	Oligochaeta	1	0.0013		Sphaeridae	38	0.0007		Oligochaeta	49	0.0019
1mm	Chironomidae (P)	1	--		Nematoda	12	--		Acari	7	0.0002
	Chironomidae (L)	30	0.0037		Trichoptera	1	--		Ostracoda	114	--
	Hyallela	24	0.0121		Oligochaeta	13	--	total	14	1392	
	Sphaeridae	6	0.0006		Ceratopogonidae	9	--				
	Oligochaeta	6	0.0066		Ostracoda	30	--				

Table B2: continued

LLB800 May 12th, 1996				LLB800 July 28th, 1996				LLB800 August 15th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
	Ostracoda	19	--	total	13	1329		sample L5 @ 2m			
	Nematoda	1	--					4mm	Oligochaeta	1	arch
	Phryganeidae	3	1E-04					1mm	Chironomidae (L)	12	arch
250u	Chironomidae (L)	8	0.0007	sample L4 @ 2m					*Gammarus*	34	arch
	Ostracoda	88	--	4mm	Trichoptera (P)	1	0.002		*Hyallela*	16	arch
total	9	198			Oligochaeta	3	0.007		*Chaoborus*	32	arch
					Ceratopogonidae	1	0.0002		Oligochaeta	2	arch
				1mm	Chironomidae (P)	4	0.0004		Ceratopogonidae	11	arch
sample L6 @ 2m					Chironomidae (L)	138	0.0113		Sphaeridae	29	arch
4mm	*Gammarus*	1	arch		*Hyallela*	422	0.0399		Nematoda	2	arch
1mm	Chironomidae (P)	22	arch		*Gammarus*	41	0.0123		Hirudinea	5	arch
	Chironomidae (L)	357	arch		Nematoda	6	--		Acari	1	arch
	Hyallela	31	arch		Sphaeridae	13	0.0006		Ostracoda	12	arch
	Sphaeridae	45	arch		Ceratopogonidae	45	0.0092	250u	Chironomidae (L)	29	arch
	Nematode	7	arch		Lymnaeadae	2	0.0007		Oligochaeta	8	arch
	Ceratopogonidae	11	arch		Oligochaeta	15	0.0131		Sphaeridae	58	arch
	Trich:Phryganea	1	arch		Hirudinea	2	0.0061		Acari	1	arch
	Trich:immature	2	arch		Corixidae	1	0.0017		*Chaoborus*	1	arch
	Trich:Oecetis	1	arch		Trichoptera	1	--		Ceratopogonidae	3	arch
	Ostracoda	14	arch		Ostracoda	1	--		Nematoda	9	arch
250u	Chironomidae (L)	182	arch	250u	Chironomidae (P)	1	0.0004		Ostracoda	132	arch
	Chironomidae (P)	1	arch		Chironomidae (L)	1134	0.0065	total	11	398	
	Nematoda	3	arch		*Hyallela*	182	0.007				
	Sphaeridae	6	arch		Nematoda	20	--				
	Acari	3	arch		Sphaeridae	33	0.0003	sample L6 @ 2.4m			
	Ceratopogonidae	1	arch		Acari	4	--	4mm	Notonectidae	2	0.0161

Table B2: continued

LLB800 May 12th, 1996				LLB800 July 28th, 1996				LLB800 August 15th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
	Ostracoda	160	arch		Ceratopogonidae	16	0.0006		Ceratopogonidae	1	1E-04
total	12	848			Oligochaeta	29	0.0009		Oligochaeta	2	0.003
					Trichoptera	3	--	1mm	Chironomidae (L)	43	0.0022
					Ostracoda	16	--		*Gammarus*	9	0.0089
sample L8 @ 2m				total	15	2134			*Hyallela*	3	--
4mm	Molannidae	1	0.0035						*Chaoborus*	14	0.0038
	Phryganeidae	1	0.0029						Sphaeridae	11	0.0015
	Leptoceridae	1	--	sample L5 @ 2m					Ceratopogonidae	3	0.001
	Gammarus	14	0.0562	4mm	*Gammarus*	1	0.0077		Hirudinea	12	0.0068
	Oligochaeta	4	0.0139		Molannidae	1	0.0017		Oligochaeta	2	0.0022
1mm	Chironomidae (L)	277	0.0202		Oligochaeta	2	0.0009		Nematoda	2	--
	Hyallela	188	0.1031	1mm	Chironomidae (P)	4	0.0003		Ostracoda	3	--
	Ceratopogonidae	89	0.01		Chironomidae (L)	245	0.0144	250u	Chironomidae (L)	49	0.0015
	Molannidae	1	--		*Hyallela*	758	0.0653		Acari	4	0.0006
	Leptoceridae (1)	2	--		*Gammarus*	92	0.0479		Sphaeridae	19	0.0011
	Leptoceridae (2)	16	0.0024		Sphaeridae	22	0.003		Nematoda	22	--
	Sphaeridae	33	0.0042		Oligochaeta	25	0.014		Oligochaeta	3	--
	Oligochaeta	23	0.0292		Corixidae	2	0.0029		Ostracoda	117	--
	Nematoda	1	--		Ceratopogonidae	35	0.0088	total	12	321	
	Caenidae	2	--		Nematoda	5	--				
	Gammarus	2	0.0065		Ostracoda	6	--				
	Ostracoda	13	--	250u	Chironomidae (L)	636	0.0048	sample L7 @ 2.9m			
250u	Chironomidae (L)	102	0.0013		*Hyallela*	166	0.0055	4mm	Hirudinea	3	0.0776
	Ceratopogonidae	17	0.0017		Acari	4	0.0003		Notonectidae	1	0.0099
	Acari	1	--		Ceratopogonidae	12	0.0021	1mm	Chironomidae (L)	56	0.0056
	Sphaeridae	12	0.0002		Oligochaeta	9	0.0005		*Gammarus*	2	0.002

Table B2: continued

LLB800 May 12th, 1996				LLB800 July 28th, 1996				LLB800 August 15th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
	Nematoda	1	--		Sphaeridae	41	0.0002		*Chaoborus*	13	0.005
	Ostracoda	233	--		Nematoda	11	--		Hirudinea	4	0.0109
total	15	1034			Ostracoda	132	--		Sphaeridae	78	0.0062
				total	12	2209			Acari	2	--
									Ceratopogonidae	1	0.0006
sample L10 @ 2m									Oligochaeta	2	0.0002
4mm	*Gammarus*	1	0.0059	sample L8 @ 2m					Ostracoda	21	--
	Oligochaeta	2	0.0017	sieve	taxa	#/grab	drywt	250u	Chironomidae (L)	54	0.0004
1mm	Chironomidae (L)	50	0.0085	4mm	Hirudinea	1	arch		Nematoda	23	--
	Hyallela	162	0.0876		Oligochaeta	1	arch		Sphaeridae	68	0.0018
	Ceratopogonidae	91	0.0074	1mm	Chironomidae (P)	8	arch		Oligochaeta	5	--
	Sphaeridae	19	0.0014		Chironomidae (L)	205	arch		Ostracoda	112	--
	Caenidae	3	0.0001		*Hyallela*	517	arch	total	11	445	
	Oligochaeta	5	0.0082		*Gammarus*	30	arch				
	Gammarus	1	0.0025		Ceratopogonidae	12	arch				
	Leptoceridae (1)	1	--		Oligochaeta	6	arch	sample L9@1.9m			
	Leptoceridae (2)	3	--		Sphaeridae	11	arch	1mm	Chironomidae (L)	10	1E-04
	Acari	1	--		Hirudinea	6	arch		*Hyallela*	95	0.0182
	Hirudinea	1	0.0032		Acari	2	arch		*Gammarus*	16	0.0154
250u	Chironomidae (L)	27	1E-04		Ostracoda	4	arch		*Chaoborus*	27	0.0095
	Ceratopogonidae	19	0.0007	250u	Chironomidae (L)	380	arch		Sphaeridae	12	1E-04
	Sphaeridae	5	--		*Hyallela*	148	arch		HIrudinea	6	0.0081
	Nematoda	1	--		Sphaeridae	52	arch		Acari	4	0.0011
	Acari	1	--		Nematoda	15	arch		Ceratopogonidae	4	0.0002
	Ostracod	8	--		Acari	3	arch		Nematoda	2	--
total	13	401			Ceratopogonidae	4	arch		Oligochaeta	1	--

Table B2: continued

LLB800 May 12th, 1996			LLB800 July 28th, 1996				LLB800 August 15th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
					Oligochaeta	4	arch	250u	Chironomidae (L)	44	0.0012
					Ephemeroptera	1	arch		Nematoda	85	--
					Ostracoda	185	arch		Sphaeridae	25	0.0008
				total	12	1405			Oligochaeta	8	0.0006
									Ostracoda	57	--
								total	11	396	
				sample L10 @ 2m							
				1mm	Chironomidae (L)	3	--				
					Hyallela	19	0.0016				
					Sphaeridae	1	--				
					Hirudinea	3	0.0012				
					Ceratopogonidae	1	1E-04				
					Ostracoda	1	--				
				250u	Chironomidae (L)	10	1E-04				
					Hyallela	6	0.0004				
					Sphaeridae	3	0.0003				
					Ostracoda	111	--				
				total	6	158					

Table B3. SCL20 benthic macroinvertebrate density (#individuals/sample) and dry weight biomass (g/sample) data for spring 1996, late summer 1996, and late summer 1997 sampling trips.

SCL20 May 20 '96				SCL20 Aug 2 '96				SCL20 Aug 13 '97			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
sample L2 @ 2m				sample L2 @ 2m				sample L2 @ 1.8m			
4mm	Chironomidae (L)	1	0.0021	4mm	Chironomidae (L)	23	0.0232	4mm	*Gammarus*	1	0.0046
	Hyallela	1	0.0084		*Gammarus*	7	0.0198		Molannidae	2	0.0051
	Molannidae	1	0.0069		*Hyallela*	2	0.0021	1mm	Chironomidae (L)	26	0.0015
1mm	Chironomidae (L)	14	0.0005		Chironomidae (P)	1	1E-04		*Hyallela*	2	--
	Chironomidae (P)	5	0.0033	1mm	*Hyallela*	160	0.0312		Nematode	1	--
	Hyallela	25	0.0218		Chironomidae (L)	323	0.0449		Sphaeridae	3	0.0009
	Ostracoda	1	--		Sphaeridae	10	0.0052		Ceratopogonidae	1	--
	Oligochaeta	7	0.002		*Gammarus*	26	0.0374		Ostracoda	9	--
	Molannidae	1	--		Ostracoda	15	--	250u	Chironomidae (L)	56	--
	Acari	1	--		Chironomidae (P)	14	0.0025		Sphaeridae	1	--
250u	Chironomidae (L)	4	--		Oligochaeta	13	0.0002		Nematode	1	--
	Ostracoda	26	--		Nematoda	1	--		Ostracoda	212	--
	Oligochaeta	1	--	250u	Ostracoda	1320	--	total	8	315	
	Acari	1	--		Chironomidae (L)	178	0.0032				
Total	6	89			Oligochaeta	190	0.0013				
					Sphaeridae	24	0.0017	sample L4 @ 2m			
					Hyallela	10	--	4mm	*Gammarus*	1	0.0028
sample L3 @ 2m					*Gammarus*	7	--	1mm	Chironomidae (L)	26	0.0026
1mm	Chironomidae (L)	13	0.02		Nematoda	101	--		Nematoda	1	--
	Chironomidae (P)	16	0.0093	total		8 2425			Oligochaeta	2	--
	Hyallela	9	0.0111						Ostracoda	2	--
	Oligochaeta	2	1E-04					250u	Chironomidae (L)	107	0.0002
	Acari	1	--	sample L3 @ 2m					Nematoda	32	--
250u	Chironomidae (L)	19	0.0002	4mm	Chironomidae (L)	31	arch		Oligochaeta	2	--

Table B3: continued

SCL20 May 20 '96				SCL20 Aug 2 '96				SCL20 Aug 13 '97			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
	Oligochaeta	15	0.0008		Ceratopogonidae	1	arch		Ostracoda	158	--
	Acari	1	--		Limnephilidae	1	arch	total	5	331	
	Ostracoda	5	--		*Gammarus*	3	arch				
total	6	81		1mm	Chironomidae (P)	20	arch				
					Chironomidae (L)	190	arch	sample L5 @ 1.8m			
sample L4 @ 2m					Hirudinea	1	arch	4mm	Chironomidae (L)	1	1E-04
4mm	Chironomidae (L)	6	0.0089		*Hyallela*	9	arch		Molannidae	1	0.0019
	Molannidae	1	0.0004		*Gammarus*	22	arch		Hirudinea	1	0.0138
1mm	*Hyallela*	6	0.0054		Oligochaeta	10	arch	1mm	Chironomidae (L)	5	0.0003
	Chironomidae (L)	3	--		Sphaeridae	3	arch		Molannidae	5	0.0011
250u	Ephemeroptera	4	--		Molannidae	1	arch		Sphaeridae	41	0.0108
	Ostracoda	7	--	250u	Chironomidae (L)	271	arch		Oligochaeta	3	--
	Nematoda	2	0.0002		Oligochaeta	50	arch		Hirudinea	1	0.0135
	Oligochaeta	9	0.0162		Sphaeridae	7	arch		*Hyallela*	8	0.0012
	Hyallela	1	--		Ostracoda	625	arch		Ostracoda	9	--
	Chironomidae (L)	19	0.0004		Trichoptera	1	arch	250u	Chironomidae (L)	9	--
	Sphaeridae	1	--		*Hyallela*	4	arch		Sphaeridae	13	0.0004
total	8	59			Nematoda	2	arch		Nematoda	3	--
				total	13	1252			Ostracoda	118	--
sample C2 @ 2m								total	8	218	
1mm	Chironomidae (L)	3	0.0002								
	Hyallela	9	0.0099	sample L5 @ 2m							
	Ceratopogonidae	3	0.0013	4mm	*Gammarus*	34	0.0916	sample C2 @ 2.2m			
250u	Chironomidae (L)	15	--		Chironomidae (L)	13	0.001	4mm	*Gammarus*	1	0.0043
	Ostracoda	6	--		Molannidae	3	0.0074		Molannidae	1	--
	Oligochaeta	3	0.0002		Corixidae	1	0.0021		Hirudinea	1	0.0459
	Acari	1	--		*Hyallela*	1	0.0017	1mm	Chironomidae (L)	3	--

Table B3: continued

SCL20 May 20 '96				SCL20 Aug 2 '96				SCL20 Aug 13 '97			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
	Nematoda	3	--	1mm	*Hyallela*	76	0.0167		*Hyallela*	35	0.0093
total	7	43			Oligochaeta	9	0.0004		*Gammarus*	5	0.0032
					Chironomidae (L)	97	0.0096		Molannidae	4	0.0008
					Chironomidae (P)	8	0.0012		Sphaeridae	35	0.0022
Sample C3@2m					Sphaeridae	19	0.0078		Oligochaeta	1	--
4mm	Molannidae	1	arch		*Gammarus*	22	0.0369		Ostracoda	4	--
1mm	Chironomidae (L)	10	arch		Corixidae	1	--	250u	Chironomidae (L)	15	--
	Ostracoda	1	arch		Hirudinea	1	0.0038		Sphaeridae	55	0.0021
	Hyallela	1	arch		Trichoptera	4	--		Oligochaeta	5	1E-04
	Oligochaeta	2	arch		Ostracoda	5	--		Nematoda	1	--
250u	Chironomidae (L)	60	arch	250u	Ostracoda	864	--		Ostracoda	23	--
	Ostracoda	53	arch		Chironomidae (L)	209	0.003	total	9	189	
	Oligochaeta	8	arch		Oligochaeta	138	0.0011				
	Acari	1	arch		*Hyallela*	45	0.0005				
	Sphaeridae	1	arch		Sphaeridae	39	0.0016	sample C3 @ 2m			
total	7	138			Nematoda	6	--	4mm	Molannidae	1	arch
					Acari	1	--	1mm	Chironomidae (L)	2	arch
				total	13	1596			*Hyallela*	14	arch
sample C5 @ 2m									Molannidae	8	arch
1mm	Chironomidae (L)	3	0.0011						*Gammarus*	7	arch
	Hyallela	14	0.0162	sample C2 @ 2m					Sphaeridae	17	arch
250u	Ostracoda	40	0.0005	4mm	Chironomidae (L)	8	0.0039		Oligochaeta	1	arch
	Chironomidae (L)	18	--		*Gammarus*	1	0.003		Ostracoda	1	arch
	Acari	3	--		*Hyallela*	2	0.0018	250u	Chironomidae (L)	17	arch
	Oligochaeta	2	0.0003		Molannidae	1	0.0051		Sphaeridae	18	arch
total	5	80		1mm	Chironomidae (L)	88	0.0114		Oligochaeta	3	arch
					Hyallela	166	0.0226		Nematoda	1	arch

Table B3: continued

SCL20 May 20 '96			SCL20 Aug 2 '96				SCL20 Aug 13 '97			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
					Sphaeridae	5	0.0015		*Gammarus*	1	arch
					Ostracoda	3	--		Ostracoda	7	arch
					Oligochaeta	3	--	total	8	98	arch
					Gammarus	17	0.0103				
					Chironomidae (P)	5	0.0007				
					Molannidae	1	--	sample C4 @ 2m			
					Acari	1	--	1mm	Chironomidae (L)	6	0.0007
					Corixidae	1	--		*Hyallela*	17	0.0061
					Nematoda	1	--		Sphaeridae	36	0.0042
				250u	Chironomidae (L)	151	0.0014		Molannidae	1	--
					Oligochaeta	58	--		*Gammarus*	4	0.0035
					Acari	4	--		Ostracoda	2	--
					Ostracoda	221	--	250u	Chironomidae (L)	17	--
					Hyallela	46	0.0009		Sphaeridae	11	0.0005
					Nematoda	87	--		Nematoda	7	--
					Sphaeridae	6	--		Ostracoda	44	--
				total	11	876	--	total	7	145	
				sample C3 @ 2m							
				4mm	Chironomidae (L)	4	0.0015				
					Gammarus	9	0.0226				
				1mm	Chironomidae (L)	70	0.0103				
					Gammarus	15	0.0309				
					Hyallela	44	0.0097				
					Oligochaeta	5	--				
					Chironomidae (P)	9	0.0005				

Table B3: continued

SCL20 May 20 '96			SCL20 Aug 2 '96				SCL20 Aug 13 '97		
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve taxa	#/grab	weight (g)
					Ostracoda	2	--			
				250u	Chironomidae (L)	206	0.0034			
					Oligochaeta	37	--			
					Hyallela	8	--			
					Ostracoda	571	--			
					Sphaeridae	4	--			
					Trichoptera	2	--			
				total	8	986				
				sample C5 @ 2m						
				4mm	Gammarus	2	0.0014			
					Hirudinea	1	0.0347			
					Chironomidae (L)	3	0.0024			
					Hyallela	1	0.003			
					Oligochaeta	1	0.0005			
				1mm	Chironomidae (P)	1	--			
					Chironomidae (L)	38	0.0029			
					Hyallela	85	0.0103			
					Gammarus	18	0.0114			
					Sphaeridae	9	--			
					Trich:Limnephilidae:Limnephilus	1	--			
					Acari	2	0.0004			
					Oligochaeta	1	0.0005			
				250u	Chironomidae (L)	110	0.0011			
					Oligochaeta	25	--			
					Hyallela	36	0.0014			

Table B3: continued

SCL20 May 20 '96			SCL20 Aug 2 '96				SCL20 Aug 13 '97			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
					Sphaeridae	43	0.0009				
					Nematoda	21	--				
					Acari	51	0.0012				
					Ostracoda	18	--				
				total	11	467					

Table B4. SCL800 benthic macroinvertebrate density (#individuals/sample) and dry weight biomass (g/sample) data for spring 1996, late summer 1996, and late summer 1997 sampling trips.

SCL800 May 21st, 1996				SCL800 August 1st, 1996				SCL800 Aug 13th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
sample L1 @ 2m				sample L1 @ 2m				sample L2 @ 2.2m			
4mm	Corduliidae	1	0.0235	4mm	*Gammarus*	3	0.0117	1mm	Chironomidae (L)	85	0.003
	Molannidae	1	0.0002		Ceratopogonidae	1	1E-04		Chironomidae (P)	2	
1mm	Chironomidae (L)	64	0.0059	1mm	Chironomidae (L)	221	0.0082		Ceratopogonidae	7	0.003
	Ceratopogonidae	1	0.0006		Chironomidae (P)	9	0.0003		*Chaoborus*	2	--
	Chaoborus	3	0.0006		Acari	6	0.0004		Hirudinea	1	--
	Sphaeridae	22	0.0034		Ostracoda	11	--		Acari	1	--
	Molannidae	1	0.0003		Planorbidae	26	0.0051	total	7	98	
	Hirudinea	2	0.001		Caenidae	1	--				
	Hyallela	1	0.0002		*Chaoborus*	2	--				
250u	Chironomidae (L)	1	--		*Hyallela*	6	0.0003	sample L5 @ 1.9m			
	Sphaeridae	3	--		Hirudinea	1	0.0003	4mm	Corduliidae	2	arch
	Ostracoda	1	--	250u	Chironomidae (L)	251	0.004	1mm	Chironomidae (L)	229	arch
total	9	101			Chironomidae (P)	1	--		Chironomidae (P)	3	arch
					Acari	19	0.0014		Caenidae	1	arch
					Planorbidae	12	0.0005		Hirudinea	2	arch
sample L2 @ 2m					Oligochaeta	4	0.0005		Ceratopogonidae	1	arch
4mm	Ceratopogonidae	9	0.0033		Ostracoda	99	--		Conchostraca	1	arch
	Gammarus	1	0.0094	total	12	673			*Hyallela*	1	arch
	Hyallela	1	0.0007						Tipulidae	1	arch
	Hirudinea	1	0.0245						*Chaoborus* (tails)	1	arch
	Caenidae	1	1E-04	sample L3 @ 2m					Nematoda	1	arch
1mm	Chironomidae (L)	111	0.0105	1mm	Chironomidae (L)	148	0.0056		Acari	2	arch
	Sphaeridae	32	0.008		Chironomidae (P)	2	--	total	12	245	
	Ostracoda	38	--		Ostracoda	31	--				

Table B4: continued

SCL800 May 21st, 1996				SCL800 August 1st, 1996				SCL800 Aug 13th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
	Caenidae	3	0.0002		Ceratopogonidae	1	0.0002				
	Acari	11	0.001		Planorbidae	18	0.0022	sample L7 @ 2.5m			
	Nematoda	2	--		*Hyallela*	6	0.0013	1mm	Chironomidae (L)	83	0.0045
	Chaoborus	1	0.0003		Hirudinea	1	0.0005		Chironomidae (P)	1	--
	Ceratopogonidae	1	--		Acari	4	--		*Chaoborus*	3	--
	HIrudinea	1	0.0004	250u	Chironomidae (L)	97	0.0012		Sphaeridae	6	0.0012
	Hyallela	1	0.0061		Planorbidae	11	1E-04		Acari	1	0.0003
250u	Chironomidae (L)	75	--		Ostracoda	128	--		*Hyallela*	1	--
	Acari	34	0.001		Chironomidae (P)	1	--		Oligochaeta	1	--
	Sphaeridae	6	0.0021		Acari	13	0.0003	total	7	96	
	Ostracoda	116	--		*Hyallela*	3	--				
	Caenidae	2	--		Oligochaeta	1	--				
total	11	447			Caenidae	2	--	sample L8 @ 2.5m			
				total	10	467		1mm	Chironomidae (L)	184	0.0106
									Sphaeridae	20	0.0064
sample L3 @ 2m									*Chaoborus*	3	0.0001
4mm	Chironomidae (L)	3	arch	sample L4 @ 2m					Hirudinea	2	0.0005
1mm	Chironomidae (L)	48	arch	4mm	Hirudinea	2	0.0809		Oligochaeta	2	--
	Acari	7	arch	1mm	Chironomidae (L)	104	0.0045		Ceratopogonidae	1	0.0002
	Sphaeridae	3	arch		Chironomidae (P)	4	--		Acari	1	0.0002
	Ostracoda	9	arch		Sphaeridae	2	0.0011	total	7	213	
	Hyallela	5	arch		Planorbidae	8	0.0008				
	Caenidae	4	arch		Ostracoda	22	--				
	Chaoborus	1	arch		*Hyallela*	15	0.002	sample L9 @ 2.5m			
	Planorbidae	1	arch		Ceratopogonidae	1	--	1mm	Chironomidae (L)	106	0.005
	Nematoda	1	arch		Hirudinea	2	0.0003		Sphaeridae	18	0.007
	Hirudinea	1	arch		Acari	2	--		*Chaoborus*	5	0.0003

Table B4: continued

SCL800 May 21st, 1996				SCL800 August 1st, 1996				SCL800 Aug 13th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
	Oligochaeta	1	arch	250u	Chironomidae (L)	35	0.0017		Hirudinea	1	0.0006
250u	Chironomidae (L)	26	arch		Chironomidae (P)	1	0.0001		Oligochaeta	3	1E-04
	Acari	7	arch		Acari	13	0.0014	total	5	133	
	Sphaeridae	1	arch		Planorbidae	2	--				
	Ostracoda	31	arch		Ostracoda	165	--				
	Planorbidae	1	arch		Sphaeridae	3	--	sample L10 @ 2.5m			
	Oligochaeta	1	arch		Hyallela	1	--	1mm	Chironomidae (L)	103	0.0043
total	11	151			Caenidae	1	--		Chironomidae (P)	2	1E-04
				total	10	383			*Chaoborus*	8	0.0005
									Ceratopogonidae	2	1E-04
sample L4 @ 2m									Sphaeridae	12	0.0037
1mm	Chironomidae (L)	59	0.0052	sample L6 @ 2m					Oligochaeta	2	0.0001
	Acari	6	0.001	1mm	Chironomidae (L)	77	0.0061		Acari	1	--
	Sphaeridae	5	0.0005		Chironomidae (P)	2	1E-04		Corduliidae	1	0.0052
	Ostracoda	20	--		Sphaeridae	21	0.0048		Coenagrionidae	1	0.0009
	Caenidae	2	0.0003		Ostracoda	22	--	total	9	132	
	Planorbidae	2	0.0021		*Hyallela*	105	0.0229				
	Phryganeidae	1	0.0009		Planorbidae	1	--				
	Lepidostomatidae	1	0.0004		Notonectidae	1	0.0021				
	Brachycentridae	1	--		Nematoda	2	--				
	Hyallela	1	--		Ceratopogonidae	1	--				
	Hirudinea	1	0.0004	250u	Chironomidae (L)	12	0.0007				
	Chaoborus	1	--		Sphaeridae	10	0.0006				
250u	Chironomidae (L)	6	0.0006		Ostracoda	58	--				
	Sphaeridae	1	--		Oligochaeta	3	--				
	Ostracoda	28	--		Acari	1	--				
	Acari	8	0.0007	total	11	316					

Table B4: continued

SCL800 May 21st, 1996				SCL800 August 1st, 1996				SCL800 Aug 13th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
total	12	143									
				sample L8 @ 2m							
sample L6 @ 2m				1mm	Chironomidae (L)	92	arch				
4mm	Hirudinea	2	0.1632		Chironomidae (P)	2	arch				
	Spongillidae	1	0.008		Hirudinea	1	arch				
1mm	Chironomidae (L)	116	0.0113		Ostracoda	129	arch				
	Acari	5	0.0003		*Hyallela*	34	arch				
	Sphaeridae	8	0.0033		Oligochaeta	2	arch				
	Ostracoda	14	--		Ceratopogonidae	1	arch				
	Caenidae	3	0.0002		Nematoda	1	arch				
	Oligochaeta	2	0.0003		Hydroptilidae	1	arch				
	Planorbidae	2	1E-04		Planorbidae	16	arch				
	Hirudinea	1	0.0002		Sphaeridae	5	arch				
	Hyallela	11	0.0051		Acari	7	arch				
	Phryganeidae	4	--		Phryganeidae	1	arch				
250u	Chironomidae (L)	30	0.0003	250u	Chironomidae (L)	19	arch				
	Sphaeridae	3	--		Planorbidae	11	arch				
	Ostracoda	43	--		Ostracoda	315	arch				
	Acari	3	--		Sphaeridae	1	arch				
	Caenidae	1	--		Acari	2	arch				
total	11	249			Oligochaeta	3	arch				
					Hyallela	1	arch				
				total	13	644					
sample L8 @ 2m											
1mm	Chironomidae (L)	80	0.005								
	Acari	6	0.0019	sample L9 @ 2m							

Table B4: continued

SCL800 May 21st, 1996				SCL800 August 1st, 1996				SCL800 Aug 13th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
	Sphaeridae	12	0.001	1mm	Chironomidae (L)	25	0.0005				
	Ostracoda	8	--		Chironomidae (P)	1	--				
	Planorbidae	2	0.0036		Ostracoda	31	--				
	Hyallela	1	--		*Gammarus*	57	0.0094				
	Hydroptilidae	1	--		*Hyallela*	7	0.0028				
	Oligochaeta	1	--		Planorbidae	11	0.0414				
	Nematoda	1	--		Sphaeridae	5	0.0015				
	Hirudinea	1	--		Acari	2	0.0003				
250u	Chironomidae (L)	30	0.0004		Nematoda	3	--				
	Sphaeridae	2	--		Ceratopogonidae	1	--				
	Ostracoda	58	--		Hirudinea	4	0.0003				
	Acari	17	0.0004		Caenidae	1	0.0003				
	Oligochaeta	1	--		Phryganeidae	1	0.0002				
total	10	221		250u	Chironomidae (L)	8	0.0004				
					Planorbidae	9	0.0006				
					Ostracoda	105	--				
					Acari	13	--				
					Hyallela	2	--				
				total	13	286					

Table B5. SPH20 benthic macroinvertebrate density (#individuals/sample) and dry weight biomass (g/sample) data for spring 1996, late summer 1996, and late summer 1997 sampling trips.

SPH20 May 28th, 1996				SPH20 August 7th, 1996				SPH20 August 12th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
sample L1 @ 2m				sample L2 @ 2.2m				sample L3 @ 3.7m			
4mm	*Gammarus*	9	0.0442	1mm	Chironomidae (L)	17	arch	4mm	Hirudinea	1	0.0046
	Polycentropodidae	1	--		*Gammarus*	31	arch		Limnephilidae	1	0.0122
	Physidae	1	0.0187		*Hyallela*	4	arch		Trichoptera (P)	1	0.0197
	Oligochaeta	1	--		Hirudinea	1	arch	1mm	Chironomidae (P)	6	0.0005
1mm	Chironomidae (L)	49	0.0021		Sphaeridae	11	arch		Chironomidae (L)	40	0.0032
	Hyallela	13	0.0038		*Chaoborus*	4	arch		*Hyallela*	157	0.0132
	Polycentropodidae	4	0.0061		Lymnaeadae	1	arch		*Gammarus*	17	0.0039
	Nematoda	5	--		Phryganeidae	2	arch		Nematoda	6	--
	Ceratopogonidae	2	--	250u	Chironomidae (L)	50	arch		Oligochaeta	19	0.0005
	Hirudinea	2	0.0038		Trichoptera	66	arch		Polycentropodidae	1	--
	Oligochaeta	2	0.0005		Ostracoda	59	arch		Hirudinea	1	0.0027
250u	Chironomidae (L)	42	0.0012		*Hyallela*	6	arch		Ceratopogonidae	3	--
	Oligochaeta	2	--		*Chaoborus*	2	arch		Sphaeridae	4	--
	Nematoda	2	--		Sphaeridae	9	arch		Ostracoda	1	--
	Ceratopogonidae	1	--		Baetidae	4	arch	250u	Chironomidae (L)	172	0.0016
	Sphaeridae	1	--		Odonata	2	arch		*Hyallela*	48	0.0014
total	10	137			Oligochaeta	2	arch		Hirudinea	1	--
					Chloroperlidae	2	arch		Nematoda	40	--
					Nematoda	1	arch		Sphaeridae	2	--
sample L4 @ 2m				total	15	274			Oligochaeta	13	--
4mm	Tipulidae	1	0.0008						Acari	3	--
	Lymnaeadae	1	0.0055	sample L3 @ 2.9m					Ephemeroptera	1	--
	Gammarus	1	0.004	1mm	Chironomidae (L)	67	0.0078		Ostracoda	36	--
1mm	Chironomidae (L)	12	0.0016		*Hyallela*	82	0.0156	total	15	574	

Table B5: continued

SPH20 May 28th, 1996				SPH20 August 7th, 1996				SPH20 August 12th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
	Hyallela	29	0.0102		*Gammarus*	10	0.004				
	Acari	1	--		Oligochaeta	2	0.0021				
	Sphaeridae	3	0.0005		Sphaeridae	7	#REF!	sample L4 @ 3.1m			
250u	Chironomidae (L)	20	0.0005		Ceratopogonidae	1	--	4mm	Hirudinea	1	0.034
	Oligochaeta	1	--		Molannidae	5	0.0002	1mm	Chironomidae (L)	23	0.0024
total	8	69			Ostracoda	1	--		*Hyallela*	82	0.007
					Snail	1	0.0035		*Gammarus*	29	0.0111
					Chaoborus	1	--		Trichoptera	1	--
sample L5 @ 2m					Hirudinea	1	--		Oligochaeta	3	0.0034
4mm	Odonata	1	0.0906	250u	Chironomidae (L)	61	0.0013		Nematoda	2	--
	Gammarus	7	0.0302		*Hyallela*	85	0.0013		Sphaeridae	6	0.0004
	Trich:Polycentropodidae	4	0.0118		Sphaeridae	13	--		Hirudinea	2	0.0027
1mm	Chironomidae (L)	99	0.0077		Molannidae	2	--		Acari	1	--
	Hyallela	18	0.0063		Acari	2	--		Polycentropodidae	1	--
	Polycentropodidae	6	0.0064		Ceratopogonidae	2	--		Ostracoda	8	--
	Ephemeroptera	1	0.0018		Ostracoda	111	--	250u	Chironomidae (L)	43	0.0008
	Sphaeridae	17	0.0023	total	12	454			*Hyallela*	35	0.0002
	Nematoda	2	--						Nematoda	34	--
	Oligochaeta	1	0.0002	sample L4 @ 2.8m					Hirudinea	14	--
250u	Chironomidae (L)	217	0.0059	1mm	Chironomidae (L)	33	0.0017		Acari	2	--
	Sphaeridae	4	--		*Gammarus*	3	0.0002		Ostracoda	45	--
	Ceratopogonidae	1	--		Platyhelminthes	7	0.0016	total	11	332	
	Oligochaeta	5	--		Lymnaeadae	4	0.0041				
total	10	383			Planorbidae	1	1E-04				
					Chaoborus	4	--	sample L6 @ 3.9m			
sample C2 @ 2m					Sphaeridae	11	0.0065	1mm	Chironomidae (P)	1	--
1mm	Chironomidae (L)	9	0.0006		Oligochaeta	5	--		Chironomidae (L)	10	0.0016

Table B5: continued

SPH20 May 28th, 1996				SPH20 August 7th, 1996				SPH20 August 12th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
	Hyallela	13	0.0047		Molannidae	1	0.0006		*Hyallela*	76	0.0062
	Sphaeridae	22	0.0038		Polycentropodidae	5	--		*Gammarus*	40	0.0119
	Polycentropodidae	1	0.001		Trichoptera	1	--		Platyhelminthes	6	0.003
	Platyhelminthes	1	--		Ephemeroptera	1	--		Hirudinea	2	0.0036
	Chaoborus	1	--		Ceratopogonidae	1	--		Sphaeridae	5	0.0005
	Tipulidae	2	--		Ostracoda	1	--		Oligochaeta	2	--
	Oligochaeta	3	1E-04		Hirudinea	1	--		Snail	1	0.0007
250u	Chironomidae (L)	11	0.0002		Chrysomelidae (P)	1	0.0005	250u	Chironomidae (L)	24	0.001
	Oligochaeta	1	--		Chironomidae (P)	1	--		*Hyallela*	16	0.0004
	Ostracoda	4	--		Acari	1	--		Sphaeridae	11	0.0004
	Ceratopogonidae	1	--	250u	Chironomidae (L)	59	0.0023		Oligochaeta	9	--
	Sphaeridae	4	--		Nematoda	1	--		Acari	2	--
total	10	73			Platyhelminthes	1	--		Ceratopogonidae	1	--
					Ephemeroptera	3	--		Platyhelminthes	1	--
					Oligochaeta	6	--		*Gammarus*	1	--
					Ostracoda	87	--		Ostracoda	4	--
sample C3 @ 2m					Trichoptera	5	--	total	12	212	
4mm	*Gammarus*	3	0.0124		Sphaeridae	13	0.0007				
	Chaoborus	1	1E-04	total	19	257					
1mm	Chironomidae (L)	54	0.0045					sample C1 @ 3.8m			
	Hyallela	6	0.002					4mm	*Gammarus*	3	arch
	Gammarus	1	0.0033	sample C2 @ 2.9m					Oligochaeta	2	arch
	Oligochaeta	2	--	4mm	Oligochaeta	1	0.0012		Ceratopogonidae	1	arch
250u	Chironomidae (L)	65	0.0017		Hirudinea	1	0.0014	1mm	Chironomidae (L)	12	arch
	Nematoda	5	--	1mm	Chironomidae (P)	1	--		*Hyallela*	57	arch
	Ostracoda	2	--		Chironomidae (L)	37	0.0016		*Gammarus*	74	arch
	Oligochaeta	2	--		*Hyallela*	14	--		Oligochaeta	3	arch

Table B5: continued

SPH20 May 28th, 1996				SPH20 August 7th, 1996				SPH20 August 12th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
total	7	141			*Gammarus*	31	0.0153		Hirudinea	5	arch
					Oligochaeta	7	0.0027		Sphaeridae	40	arch
					Sphaeridae	17	0.0059		Platyhelminthes	3	arch
sample C4 @ 2m					Hirudinea	9	0.0033		Nematoda	1	arch
4mm	Chironomidae (L)	1	arch		Odonata	1	--		Polycentropodidae	1	arch
	Chrysomelidae	1	arch		Snail	2	0.0003		Acari	1	arch
1mm	Chironomidae (L)	12	arch		*Chaoborus*	1	--		Ostracoda	4	arch
	Hyallela	1	arch		Ephemeroptera	1	0.0009		Ceratopogonidae	1	arch
	Sphaeridae	2	arch		Ostracoda	4	--	250u	Chironomidae (L)	12	arch
250u	Chironomidae (L)	17	arch		Phryganeidae	2	0.0001		*Hyallela*	12	arch
	Ostracoda	3	arch	250u	Chironomidae (P)	1	--		Sphaeridae	92	arch
total	5	37	arch		Chironomidae (L)	44	0.0002		Nematoda	3	arch
					Hyallela	9	0.0007		Platyhelminthes	1	arch
					Sphaeridae	21	0.0006		Ostracoda	56	arch
					Acari	3	--	total	12	384	
					Nematoda	5	--				
					Oligochaeta	7	--				
					Trichoptera	10	0.0007				
					Chaoborus	2	--				
					Odonata	1	--	sample C2 @ 3.9m			
					Ostracoda	154	--	4mm	Oligochaeta	1	0.001
				total	17	386		1mm	Chironomidae (L)	7	0.0003
									Hyallela	50	0.0033
									Gammarus	22	0.0077
				sample C3 @ 3m					Sphaeridae	27	0.0024
				1mm	Chironomidae (L)	44	0.0019		*Chaoborus*	3	--
					Hyallela	25	0.0031		Oligochaeta	6	--

Table B5: continued

SPH20 May 28th, 1996				SPH20 August 7th, 1996				SPH20 August 12th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
					Ceratopogonidae	4	--		Platyhelminthes	3	--
					Gammarus	21	0.0089		Hirudinea	5	0.0039
					Sphaeridae	5	0.0008		Nematoda	2	--
					Chaoborus	3	--		Ostracoda	2	--
					Hirudinea	1	0.0002	250u	Chironomidae (L)	8	--
					Acari	1	--		*Hyallela*	13	0.0002
				250u	Chironomidae (L)	60	0.0012		Sphaeridae	29	0.0017
					Hyallela	27	0.0008		Oligochaeta	7	0.001
					Oligochaeta	7	--		Nematoda	1	--
					Ceratopogonidae	1	--		Acari	3	--
					Sphaeridae	1	--		Ostracoda	121	--
					Trichoptera	4	--	total	11	310	
					Chaoborus	1	--				
					Ostracoda	105	--				
					Acari	3	--	sample C4 @ 3.9m			
				total	11	313		4mm	Oligochaeta	1	0.0035
								1mm	Chironomidae (L)	38	0.001
									Hyallela	75	0.0047
				sample C4 @ 3m					*Gammarus*	39	0.0142
				4mm	Hirudinea	1	0.0179		Oligochaeta	3	--
				1mm	Chironomidae (L)	46	0.0054		Lymnaeadae	1	0.0009
					Hyallela	32	0.003		Sphaeridae	15	0.0013
					Gammarus	22	0.0098		Ceratopogonidae	1	--
					Platyhelminthes	1	--		*Chaoborus*	1	--
					Hirudinea	6	0.0032		Ostracoda	4	--
					Ceratopogonidae	3	--	250u	Chironomidae (L)	226	0.0021
					Acari	2	--		*Hyallela*	20	0.0018

Table B5: continued

SPH20 May 28th, 1996				SPH20 August 7th, 1996				SPH20 August 12th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
					Sphaeridae	7	0.0006		Sphaeridae	21	0.0003
					Oligochaeta	2	--		Oligochaeta	5	--
					Trichoptera	1	--		Nematoda	6	--
				250u	Chironomidae (L)	257	0.001		Acari	2	--
					Hyallela	44	0.0006		Ostracoda	55	--
					Sphaeridae	7	--		Trichoptera	1	--
					Oligochaeta	11	--	total	12	514	
					Ceratopogonidae	4	--				
					Chaoborus	1	--				
					Trichoptera	3	--				
					Acari	5	--				
					Nematoda	4	--				
					Ostracoda	38	--				
					Chironomidae (P)	1	--				
				total	14	498					

Table B6. SPH800 benthic macroinvertebrate density (#individuals/sample) and dry weight biomass (g/sample) data for spring 1996, late summer 1996, and late summer 1997 sampling trips.

SPH800 May 26th, 1996				SPH800 August 5th, 1996				SPH800 August 11th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
sample L1 @ 2m				sample L1 @ 2.4m				sample L2 @ 2.4m			
4mm	Ostracoda	49	--	4mm	Ceratopogonidae	2	arch	4mm	*Gammarus*	8	0.022
	Chironomidae (L)	1	0.0004		Nematoda	1	arch		Ceratopogonidae	2	1E-04
	Chaoborus	1	--	1mm	Chironomidae (L)	120	arch	1mm	Chironomidae (L)	178	0.0045
	Ceratopogonidae	4	0.0047		*Hyallela*	2	arch		*Hyallela*	50	0.0143
	Sphaeridae	1	0.0034		Sphaeridae	20	arch		*Gammarus*	35	0.059
1mm	Ostracoda	48	--		Ostracoda	160	arch		Ostracoda	4	--
	Chironomidae (L)	158	0.0137		Planorbidae	1	arch		Sphaeridae	91	0.0402
	Chironomidae (P)	18	0.001	250u	Chironomidae (L)	36	arch		Oligochaeta	1	--
	Sphaeridae	35	0.0102		Acari	1	arch		Ceratopogonidae	4	1E-04
	Chaoborus	16	0.0023		Sphaeridae	10	arch		*Chaoborus*	1	--
	Ceratopogonidae	11	0.0017		Ostracoda	479	arch		Planorbidae	12	0.011
	Polycentropodidae	1	0.0027		*Chaoborus*	1	arch		Hirudinea	1	--
	Hirudinea	1	--	total	9	833		250u	Chironomidae (L)	249	0.0021
	Oligochaeta	7	--						Sphaeridae	23	0.0005
	Acari	3	0.0008						Ostracoda	239	--
	Nematoda	2	--	sample L3 @ 2m					Oligochaeta	6	0.0012
	Caenidae	2	--	4mm	Ceratopogonidae	10	0.0066		Acari	1	--
	Planorbidae	2	0.0006	1mm	Chironomidae (L)	139	0.0098	total	11	905	
	Hyallela	8	0.0074		Sphaeridae	32	0.0051				
250u	Chironomidae (L)	52	1E-04		Ostracoda	39	--				
	Oligochaeta	15	0.0004		Chironomidae (P)	5	0.0002	sample L3 @ 2.2m			
	Sphaeridae	21	0.0003		Planorbidae	1	0.0017	4mm	*Gammarus*	6	0.0112
	Ostracoda	661	--		*Hyallela*	1	--		Ceratopogonidae	6	0.0069
	Acari	2	--	250u	Chironomidae (L)	73	0.0003		Unionidae	1	--

Table B6: continued

SPH800 May 26th, 1996				SPH800 August 5th, 1996				SPH800 August 11th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
	Caenidae	2	--		Acari	2	1E-04		Chironomidae (L)	1	0.0005
total	14	1121			Sphaeridae	28	0.0003	1mm	Chironomidae (L)	187	0.0074
					Ostracoda	449	--		Planorbidae	4	0.0009
				total	8	779			Ostracoda	1	--
sample L3 @ 2m									*Hyallela*	8	0.0026
1mm	Ostracoda	106	--						Sphaeridae	67	0.032
	Chironomidae (L)	96	0.0058						Acari	3	0.0002
	Chironomidae (P)	2	--	sample L5 @ 2m					Hirudinea	13	0.0029
	Ceratopogonidae	5	--	4mm	Corduliidae	1	0.0083		Oligochaeta	2	--
	Chaoborus	5	--		Sphaeridae	5	0.0415		*Gammarus*	4	0.0055
	Hirudinea	1	--		Planorbidae	1	0.0119		Ceratopogonidae	1	0.0002
	Caenidae	4	--		Chironomidae (L)	1	--	250u	Chironomidae (L)	392	0.0039
	Sphaeridae	102	0.0346	1mm	Chironomidae (L)	199	0.0094		Oligochaeta	19	0.0004
	Nematoda	1	--		Sphaeridae	70	0.1134		Sphaeridae	23	0.0006
250u	Ostracoda	1286	--		Ostracoda	46	--		Ostracoda	144	--
	Chironomidae (L)	153	0.0019		Chironomidae (P)	1	--		Amphipoda	1	--
	Chironomidae (P)	2	--		Planorbidae	9	0.0103		Acari	1	--
	Chaoborus	6	--		Lymneadae	1	0.006		Hirudinea	1	--
	Sphaeridae	183	0.004		Acari	3	--	total	12	885	
	Planorbidae	6	--		Ceratopogonidae	2	0.0002				
	Acari	9	0.0003		Oligochaeta	1	--				
	Caenidae	6	--	250u	Chironomidae (L)	179	0.0019				
	Oligochaeta	2	--		Sphaeridae	6	--	sample L5 @ 2.5m			
total	12	1975			Ostracoda	1485	--	4mm	Ceratopogonidae	6	0.0053
					Planorbidae	1	--		*Gammarus*	4	0.0074
					Acari	3	--		Hirudinea	1	0.02
sample L5 @ 2m					Oligochaeta	4	--		Unionidae	1	--

Table B6: continued

SPH800 May 26th, 1996				SPH800 August 5th, 1996				SPH800 August 11th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
4mm	Chironomidae (L)	3	0.0014	total	9	2018		1mm	Chironomidae (L)	460	0.012
	Ceratopogonidae	2	0.0015						Ostracoda	22	--
	Corduliidae	1	0.004						Sphaeridae	167	0.0452
	Sphaeridae	2	0.017	sample L6 @ 2m					*Hyallela*	88	0.0234
	Gammarus	4	0.0406	4mm	Ceratopogonidae	1	0.0003		*Gammarus*	21	0.0287
1mm	Ostracoda	411	--	1mm	Chironomidae (L)	517	0.0343		Ceratopogonidae	7	0.0028
	Chironomidae (L)	202	0.0107		Chironomidae (P)	6	0.0003		*Chaoborus*	2	1E-04
	Chironomidae (P)	9	--		Sphaeridae	100	0.0661		Planorbidae	8	0.0079
	Planorbidae	2	1E-04		Acari	9	0.0005		Nematoda	1	--
	Caenidae	5	--		Planorbidae	4	0.002	250u	Chironomidae (L)	578	0.007
	Nematoda	5	--		Oligochaeta	3	--		Acari	4	--
	Acari	7	0.0017		Caenidae	1	0.0003		Sphaeridae	73	0.0035
	Chaoborus	4	--		Ceratopogonidae	1	--		Ostracoda	1420	--
	Ceratopogonidae	3	0.0002	250u	Chironomidae (L)	211	0.0012		Oligochaeta	2	--
	Hyallela	9	0.0086		Chironomidae (P)	1	--	total	12	2865	
250u	Chironomidae (L)	26	0.0003		Sphaeridae	56	0.0029				
	Nematoda	2	--		Ostracoda	1652	--				
	Sphaeridae	61	0.0028		Acari	27	0.0004	sample L7 @ 2.5m			
	Ostracoda	1311	--		Oligochaeta	7	0.0004	4mm	Corduliidae	1	0.0357
	Oligochaeta	2	--		Hemiptera	1	1E-04		Ceratopogonidae	22	0.0203
	Acari	3	--		Ceratopogonidae	1	--		*Gammarus*	4	0.0111
	Ceratopogonidae	1	--	total	10	2597			Chironomidae (L)	1	0.0043
total	14	2075						1mm	Chironomidae (L)	1112	0.0296
									Chironomidae (P)	2	--
				sample L7 @ 2m					Sphaeridae	171	0.0309
sample L6 @ 2m				4mm	Corduliidae	1	0.0154		Ostracoda	99	--
4mm	Ceratopogonidae	1	--		Phryganeidae	1	0.0025		Ceratopogonidae	23	0.0031

Table B6: continued

SPH800 May 26th, 1996				SPH800 August 5th, 1996				SPH800 August 11th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
1mm	Chironomidae (L)	167	0.0121		Physidae	1	0.01		Planorbidae	6	0.0047
	Chironomidae (P)	7	--	1mm	Chironomidae (L)	361	0.0161		*Chaoborus*	6	0.0006
	Sphaeridae	39	0.0051		Chironomidae (P)	10	0.0013		*Hyallela*	3	0.0003
	Chaoborus	13	0.0014		Sphaeridae	7	0.0013		Hirudinea	4	0.0011
	Planorbidae	5	0.0029		Ostracoda	47	--		Nematoda	19	--
	Ostracoda	46	--		Ceratopogonidae	2	--		Acari	2	--
	Caenidae	2	--		Oligochaeta	2	0.0003	250u	Chironomidae (L)	661	0.0076
	Ceratopogonidae	2	--		Nematoda	1	--		Sphaeridae	58	0.0016
	Oligochaeta	2	--		Coenogrionidae	1	0.0007		Ostracoda	3200	--
250u	Chironomidae (L)	34	0.0009		Planorbidae	5	--		*Chaoborus*	2	1E-04
	Chironomidae (P)	1	--		Acari	4	--		Acari	1	--
	Sphaeridae	15	0.001		Zygoptera	1	--		Oligochaeta	3	--
	Ostracoda	187	--		Trichoptera	4	--		Nematoda	2	--
	Caenidae	2	--		*Hyallela*	2	--	total	14	5402	
	Oligochaeta	2	--	250u	Chironomidae (L)	179	0.0014				
total	9	525			Sphaeridae	4	--				
					Ostracoda	152	--	sample L8 @ 2.1m			
					Acari	12	0.0013	4mm	Unionidae	3	--
sample L7 @ 2m					Planorbidae	3	--		Chironomidae (L)	2	--
4mm	Corduliidae	5	arch		*Hyallela*	1	--		Ceratopogonidae	2	0.0002
	Coenogrionidae	1	arch		Oligochaeta	2	--		Sphaeridae	4	0.0247
1mm	Chironomidae (L)	233	arch		Caenidae	1	--		*Gammarus*	4	0.0064
	Chironomidae (P)	5	arch	total	17	804			Notonectidae	1	0.0088
	Sphaeridae	23	arch					1mm	Chironomidae (L)	180	0.0072
	Ostracoda	26	arch						Sphaeridae	101	0.0556
	Polycentropodidae	3	arch	sample L8 @ 2m					*Hyallela*	134	0.0798
	Planorbidae	6	arch	4mm	Chironomidae (L)	5	0.0016		Ceratopogonidae	4	0.0011

Table B6: continued

SPH800 May 26th, 1996				SPH800 August 5th, 1996				SPH800 August 11th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
	Ceratopogonidae	4	arch		Ceratopogonidae	1	--		Ostracoda	190	--
	Corduliidae	1	arch	1mm	Chironomidae (L)	206	0.0104		Planorbidae	6	0.0015
	Coenagrionidae	3	arch		Chironomidae (P)	5	0.0006		*Gammarus*	14	0.0179
	Acari	13	arch		Sphaeridae	27	0.0043		Hirudinea	11	0.0044
	Caenidae	3	arch		Ostracoda	68	--		Acari	3	1E-04
	Oligochaeta	14	arch		Oligochaeta	6	0.0003		Oligochaeta	2	--
	Hydroptilidae	1	arch		Ceratopogonidae	4	0.0003		Caenidae	1	1E-04
250u	Chironomidae (L)	61	arch		Planorbidae	1	1E-04	250u	Chironomidae (L)	130	0.0019
	Oligochaeta	27	arch		Trichoptera	1	0.0002		Sphaeridae	29	0.0012
	Sphaeridae	2	arch		Acari	1	0.0002		Ostracoda	1109	--
	Ostracoda	133	arch	250u	Chironomidae (L)	21	0.0002		Acari	16	--
	Acari	8	arch		Sphaeridae	2	--		Oligochaeta	6	--
	Caenidae	3	arch		Ostracoda	255	--		*Hyallela*	2	--
total	13	302			Trichoptera	1	--		*Gammarus*	1	0.0002
				total	9	604		total	13	1955	
sample L8 @ 2m								sample L9 @ 2.3m			
4mm	Polycentropodidae	3	0.0025					4mm	Sphaeridae	6	arch
	Corduliidae	1	0.0018						Ceratopogonidae	4	arch
	Trichoptera (P)	1	0.0127						Chironomidae (L)	59	arch
1mm	Chironomidae (L)	114	0.0032						Notonectidae	1	arch
	Chironomidae (P)	3	--					1mm	Chironomidae (L)	1012	arch
	Sphaeridae	39	0.0022						Chironomidae (P)	8	arch
	Ostracoda	74	--						Sphaeridae	123	arch
	Ceratopogonidae	9	0.0008						*Hyallela*	14	arch
	Chaoborus	3	--						Ostracoda	21	arch
	Planorbidae	2	0.0002								

Table B6: continued

SPH800 May 26th, 1996				SPH800 August 5th, 1996				SPH800 August 11th, 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
	Caenidae	4	--						Planorbidae	30	arch
	Coenogrionidae	2	--						Ceratopogonidae	7	arch
	Acari	1	--						Hirudinea	12	arch
	Oligochaeta	7	0.0007						*Gammarus*	1	arch
	Nematoda	1	--						Oligochaeta	4	arch
	Hyallela	1	0.0002						Acari	1	arch
250u	Chironomidae (L)	232	0.0019						Nematoda	1	arch
	Chironomidae (P)	2	--					250u	Chironomidae (L)	789	arch
	Sphaeridae	23	0.0002						Chironomidae (P)	1	arch
	Ostracoda	469	--						Sphaeridae	108	arch
	Oligochaeta	14	--						Ostracoda	3568	arch
	Acari	13	--						Oligochaeta	19	arch
	Caenidae	5	--						Amphipoda	1	arch
	Nematoda	1	--					total	14	5787	
	Chaoborus	1	--								
total	16	1025									

Table B7. SPH100 benthic macroinvertebrate density (#individuals/sample) and dry weight biomass (g/sample) data for late summer 1996 and late summer 1997 sampling trips.

SPH100 August 6th, 1996				SPH100 August 12 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
sample L1 @ 2m				sample L1 @ 2m			
4mm	Hirudinea	1	0.0492	1mm	*Chaoborus* (P)	1	arch
1mm	Chironomidae (P)	3	0.0006		Chironomidae (L)	27	arch
	Chironomidae (L)	300	0.0178		*Chaoborus*	119	arch
	Hirudinea	4	0.0022		Acari	4	arch
	Oligochaeta	1	--		Sphaeridae	3	arch
	Chaoborus	3	--		Oligochaeta	1	arch
	Acari	1	--		Hirudinea	1	arch
	Sphaeridae	1	0.0001		Ceratopogonidae	2	arch
total	8	314	0.0699		Nematoda	2	arch
				total	9	160	
sample L2 @ 2m							
4mm	Hirudinea	1	0.0321	sample L4 @ 2m			
1mm	Chironomidae (P)	1	--	1mm	Chironomidae (L)	53	0.0033
	Chironomidae (L)	174	0.0108		*Chaoborus*	102	0.0061
	Chaoborus	43	0.0032		Ceratopogonidae	1	--
	Hirudinea	1	0.0003		Oligochaeta	1	--
	Ceratopogonidae	2	--		Nematoda	1	--
	Acari	4	0.001		Acari	2	0.0004
	Sphaeridae	1	1E-04	total	6	160	0.0098
	Oligochaeta	5	0.0008				
total	8	232	0.0483				
				sample L5 @ 2m			
				1mm	Chironomidae (L)	25	0.0031
sample L4 @ 2m					*Chaoborus*	46	0.0047
1mm	Chironomidae (P)	1	1E-04		Sphaeridae	2	0.0013
	Chironomidae (L)	115	0.0052		Nematoda	1	--
	Sphaeridae	4	0.0009		Oligochaeta	1	0.0001
	Ceratopogonidae	3	0.0029		Acari	1	0.0002
	Chaoaborus	3	0.0003	total	6	76	0.0094
	Acari	3	0.0007				
	Oligochaeta	2	0.0008				
	Nematoda	1	--	sample C1 @ 2m			
total	8	132	0.0109	1mm	Chironomidae (L)	24	0.003
					Chaoborus	123	0.0143
					Hyallela	1	0.0005
sample C2 @ 2m					Acari	2	0.0003
1mm	Chironomidae (L)	50	0.0016		Oligochaeta	1	0.0005
	Chaoborus	12	0.0017		Hirudinea	3	0.0022
	Ceratopogonidae	1	--	total	6	154	0.0208
	Hirudinea	2	0.0007				
	Lymnaeadae	1	0.0018				
	Caenidae	1	--	sample C4 @ 2.3m			
	Nematoda	1	--	1mm	Chironomidae (L)	11	0.0017
total	7	68	0.0058		*Chaoborus*	125	0.0142

Table B7: Continued

SPH100 August 6th, 1996				SPH100 August 12 1997			
sieve	taxa	#/grab	weight (g)	sieve	taxa	#/grab	weight (g)
sample C3 @ 2m					*Chaoborus* (P)	4	0.0023
1mm	Chironomidae (P)	2	0.0003		Sphaeridae	2	0.0004
	Chironomidae (L)	115	0.0027		Acari	3	0.0007
	Gammarus	1	0.0017		Oligochaeta	1	0.0003
	Chaoborus	5	0.001	total	6	146	0.0196
	Acari	1	0.0001				
	Oligochaeta	1	--				
	Nematoda	3	0.0003	sample C5 @ 1.8m			
total	7	128	0.0061	1mm	Chironomidae (L)	12	0.001
					Chaoborus	96	0.0134
					Acari	1	0.0003
sample C4 @ 2m				total	3	109	0.0147
4mm	Hirudinea	1	arch				
1mm	Chironomidae (L)	100	arch				
	Chaoborus	17	arch				
	Acari	4	arch				
	Ceratopogonidae	2	arch				
	Nematoda	1	arch				
total	6	125					

Appendix C:

Littoral macroinvertebrate densities for LLB800 and SPH20 for late-summer 1995.

Table C1:Density of littoral zone benthic macroinvertebrates sampled by the TROLS core in late summer 1995.

LLB800-late summer 1995			SPH20-late summer 1995		
sieve	taxa	#/grab	sieve	taxa	#/grab
L5 @ 2.5m	July 15th, 1995		L2 @ 3m	July 20th, 1995	
1mm	*Hyallela*	94	1mm	*Hyallela*	234
	Ceratopogonidae	48		Chironomidae (L)	73
	Sphaeridae	16		*Gammarus*	9
	Oligochaeta	12		Hirudinea	2
	Chironomidae (L)	3		Sphaeridae	13
	Trichoptera	5		Oligochaeta	1
	Nematoda	2		Trichoptera	4
	Snail	1	total	7	336
total	8	181			
			L3 @ 2.5m	July 20th, 1995	
L3 @ +/- 2m	July 15th, 1995		1mm	*Hyallela*	110
1mm	*Hyallela*	537		*Gammarus*	13
	Gammarus	16		Hirudinea	1
	Sphaeridae	48		Chironomidae (L)	52
	Chironomidae (P)	1		Chironomidae (P)	1
	Chironomidae (L)	29		Oligochaeta	3
	Ceratopogonidae	13		Sphaeridae	5
	Chaoborus	1		Ceratopogonidae	1
	Oligochaeta	8		Acari	1
	Hirudinea	1		Tipulidae	1
	Acari	2		*Chaoborus* (tails)	2
total	10	656		Snails	2
			total	12	192
L1 @ +\-2m	August 4th 1995				
1mm	*Hyallela*	59	L1 @ 2.3m	August 11th, 1995	
	Chironomidae (L)	50	1mm	*Hyallela*	273
	Chironomidae (P)	1		*Gammarus*	85
	Nematodes	16		Trichoptera	25
	Sphaeridae	17		Sphaeridae	20
	Chaoborus	4		Chironomidae	52
	Ceratopogonidae	4		Oligochaeta	8
	Oligochaeta	3		Snails	1
	Trichoptera	5		Platyhelminthes	18
	Caenidae	1		Hirudinea	2
total	10	160		Acari	1
				Odonata	3
L2 @ 2.1m	August 4th, 1995		total	11	488
1mm	*Hyallela*	111			
	Ceratopogonidae	115	L2 @ 2.2m	August 11th, 1995	
	Oligochaeta	39	1mm	*Hyallela*	228
	Chironomidae (L)	16		*Gammarus*	33
	Caenidae	14		Hirudinea	14
	Sphaeridae	29		Sphaeridae	30

Table B1: Continued

LLB800-late summer 1995			SPH20-late summer 1995		
sieve	taxa	#/grab	sieve	taxa	#/grab
	Trichoptera	27		Chironomidae	62
	Nematoda	2		Trichoptera	4
total	8	353		Ephemeroptera	2
				Oligochaeta	4
				Snail	2
				Ceratopogonidae	3
				Dytiscidae (L)	1
				Platyhelminthes	1
			total	12	384

Appendix D:

Summary data from mid-September, 1997 macrophyte transects.

Table D1. Summary data from macrophyte transects taken in mid-September, 1997, and used to estimate mean littoral zone standing macrophyte dry weight biomass.

Lake	Transect	Depth (m)	Weight (g m-2)	Lake	Transect	Depth (m)	Weight (g m-2)	Lake	Transect	Depth (m)	Weight (g m-2)
LLB20	L1	1	0.0	SCL20	L1	1	0.0	SPH20	L1	1	400.4
		2	0.0			2	0.0			2	46.5
		3	129.3			3	0.0			3	80.2
	L2	1	0.0		L2	1	0.0		L2	1	14.7
		2	86.2			2	0.0			2	0.0
		3	129.3			3	0.0			3	0.0
	C3	1	0.0		C1	1	0.0		C1	1	0.0
		2	86.2			2	86.2			2	471.5
		3	129.3			3	0.0			3	173.7
	C4	1	0.0		C2	1	43.1		C2	1	26.7
		2	86.2			2	0.0			2	225.4
		3	0.0			3	0.0			3	304.3
LLB800	L1	1	0.0	SCL800	L1	1	192.7	SPH800	L1	1	84.0
		2	0.0			2	162.9			2	0.0
		3	0.0			3	270.2			3	0.0
	L2	1	0.0		L2	1	375.8		L2	1	87.1
		2	0.0			2	256.9			2	0.0
		3	0.0			3	228.0			3	0.0
	L3	1	0.0		L3	1	268.1		L3	1	55.6
		2	86.2			2	490.9			2	192.2
		3	0.0			3	9.1			3	0.0
	L4	1	0.0		L4	1	252.1		L4	1	32.3
		2	0.0			2	225.0			2	143.5
		3	0.0			3	334.0			3	97.8

Appendix E:

Summary data from September, 1997 sediment cores.

Table E1. Summary data from sediment cores taken in Septmber, 1997, and used to estimate sediment percent water and organic content.

Lake	Cores in sample	Wet weight (g)	Dry weight1 (g)	% H2O content	Dry weight2 (g)	Ashed weight (g)	% Organic content
LLB20	L1aL1b	4.07	0.90	77.94	0.90	0.73	18.67
	L2aL2b	4.50	0.59	86.78	0.59	0.37	38.02
	C1aC1b	5.15	1.56	69.75	1.54	0.38	75.54
LLB800	C1aC1b	4.26	0.84	80.24	0.84	0.56	33.55
	L1aL1b	4.47	0.56	87.41	0.57	0.35	38.90
	L2aL2b	10.10	6.28	37.88	6.26	4.94	21.03
SCL20	L1aL1b	5.97	1.33	77.71	1.34	1.12	16.45
	C1aC1b	10.01	6.99	30.13	6.87	6.76	1.60
	C2aC2b	7.77	5.04	35.08	5.04	4.78	5.11
SCL800	L1aL1b	3.04	0.30	90.26	0.30	0.18	40.87
	L2aL2b	4.27	0.41	90.35	0.44	0.20	54.60
	L3aL3b	4.13	0.42	89.84	0.43	0.21	50.22
SPH20	L1aL1b	3.65	0.33	90.98	0.33	0.21	37.38
	L2aL2b	3.58	0.29	92.01	0.29	0.18	38.38
	C1aC1b	3.84	0.55	85.61	0.55	0.44	20.53
SPH800	L1aL1b	3.80	0.26	93.28	0.26	0.11	56.80
	L2aL2b	1.88	0.12	93.46	0.12	0.06	52.87
	L3aL3b	3.07	0.33	89.34	0.33	0.16	51.19

Appendix F:

Summary data from littoral zone slope calculations.

Table F1. Summary data measured from bathymmetric maps and used to estimate mean lake littoral zone slope.

Lake and Transect number	Surface transect length (m)	Depth (m)	Littoral zone slope (%)	Lake and Transect number	Surface transect length (m)	Depth (m)	Littoral zone slope (%)
LLB20				SCL800			
L1	348	3	0.9	L1	202.71	2	1.0
L2	50.46	3	5.9	L2	200.10	2	1.0
L3	52.2	3	5.7	L3	452.40	2	0.4
L4	160.95	3	1.9	L4	129.63	2	1.5
L5	33.06	2	6.0	L5	233.16	2	0.9
C1	113.1	3	2.7	L6	139.20	2	1.4
C2	76.56	3	3.9	L7	130.50	2	1.5
C3	24.36	2	8.2	L8	495.90	2	0.4
C4	39.15	3	7.7	L9	291.45	2	0.7
C5	26.1	2	7.7	L10	195.75	2	1.0
LLB800				SPH20			
L1	78.438	3	3.8	L1	121.5	3	2.5
L2	107.66	3	2.8	L2	218.7	3	1.4
L3	184.56	3	1.6	L3	159.3	3	1.9
L4	153.8	3	2.0	L4	125.55	3	2.4
L5	250.694	3	1.2	L5	164.7	3	1.8
L6	127.654	3	2.4	C1	108	3	2.8
L7	138.42	3	2.2	C2	102.6	3	2.9
L8	155.338	3	1.9	C3	139.05	3	2.2
L9	64.596	3	4.6	C4	54	3	5.6
L10	246.08	3	1.2	C5	108	3	2.8

Table E1: continued

Lake and Transect number	Surface transect length (m)	Depth (m)	Littoral zone slope (%)
SCL20			
L1	72.72	4	5.5
L2	121.81	4	3.3
L3	81.81	4	4.9
L4	77.27	4	5.2
L5	72.72	4	5.5
C1	72.72	4	5.5
C2	80.90	4	4.9
C3	97.26	4	4.1
C4	81.81	4	4.9
C5	57.27	4	7.0
SPH100			
L1	509.22	2	0.4
L2	639.35	2	0.3
L3	301.76	2	0.7
L4	235.75	2	0.8
L5	577.12	2	0.3
C1	462.07	2	0.4
C2	433.78	2	0.5
C3	627.10	2	0.3
C4	344.20	2	0.6
C5	130.13	2	1.5
SPH800			
L1	212	3	1.4
L2	385	3	0.8
L3	88	3	3.4
L4	160	3	1.9
L5	198	3	1.5
L6	100	3	3.0
L7	37	3	8.1
L8	35	3	8.6
L9	160	3	1.9
L10	139	3	2.2